IDENTIFICATION OF SPAWNING AREAS AND THE INFLUENCE OF ENVIRONMENTAL VARIATION ON FRESHWATER MIGRATION TIMING AND IN-RIVER MOVEMENTS OF ADULT COHO SALMON IN THE BUSKIN RIVER, ALASKA.

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Abstract

The timing of freshwater entry by anadromous salmonids varies markedly among species and populations within species and is frequently used as an indicator of local adaptation to site-specific patterns of selection. Although complex stock structure is most often associated with large watersheds that have extensive habitat diversity, even small drainages can produce multiple co-occurring stocks that differ in migratory timing. In addition, migration timing can be influenced by within-year environmental conditions experienced by migrating individuals *en route* to spawning sites, staging near the river mouth in the ocean, or within the river itself. Each stage of migration through both freshwater and saltwater could be altered based on climatic drivers and how each individual fish reacts to these stressors. The objective of this thesis was to assess the potential for stock structure in Coho Salmon within a small coastal watershed on Kodiak Island, Alaska by 1) identifying important differences in spawning and holding locations associated with run timing, length, and stream life between main stem and tributary spawners, 2) quantifying the influence of large-, intermediate-, and local-scale climate variables on freshwater entrance timing and in-river movements. To address the first objective, fish were tracked to their spawning locations using acoustic telemetry in three spawning seasons (2015-2017). I detected no statistically or biologically meaningful differences in body size (length, mm) or migration timing into the river between main stem and tributary spawning fish. Unexpectedly, I found that a large portion of fish (80%) utilize the lake during their in-river migration suggesting the lake may represent critical staging habitat for adult Coho Salmon prior to spawning. I also identified holding habitat throughout the river that both spawning groups consistently used across years that also appears to be important to premature migrating Coho Salmon. In Chapter Two, I analyzed 33 years of freshwater entrance timing data and utilized radio tags to track in-river movement to quantify the influence of precipitation and temperature on total distance moved and probability of moving. Despite marked variation among years, I found no evidence of a temporal trend in entrance timing based on escapement counts, which contrasts with other recent examples throughout Alaska reporting changes in run timing. The strongest influence on timing of freshwater entry was ocean sea surface temperature, where cold temperatures delayed entry up to 11 days. Within-river movements were positively related to precipitation and temperature, confirming local traditional knowledge in this system, and consistent with life history patterns of Coho Salmon. The primary messages of this thesis are that *i*) any within-watershed stock structure is unlikely to be differentially affected by harvest or management given overlapping run timing, body size, and use of main stem holding areas; future population genetics analyses would be an obvious and illuminating next step to assess the extent to which main stem and tributary spawners are reproductively isolated groups; *ii*) both main stem and tributary spawners use Buskin Lake as holding habitat prior to spawning, and thus assumptions that fish that enter the upper watershed are destined to spawn in headwater tributaries are invalid, which in turn limits the utility of enumerating adult passage into the lake for escapement-based management, *iii*) adult freshwater entrance timing is highly variable but not changing systematically through time, though the extent to which the variation in timing reflects environmental response vs. uncertainty in the counts at the weir is unknown, and *iv*) low precipitation and warm temperatures suppress movement and result in protracted use of main stem and lake habitats for holding, which may put some individuals at risk to angler harvest or, in extreme events, potentially low dissolved oxygen environments. Spatial management that restricts fishing in locations of known primary holding habitats may be an option to reduce probability of mortality and stress in years of low adult abundance.

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Introduction

A warming global climate system is altering a myriad of physical processes in freshwater ecosystems and creating challenges for stream-rearing fishes (Casselman 2002; Sharma et al. 2007; Isaak et al. 2010; Hartmann et al. 2013). Abiotic responses to climate change are site-specific, given the unique topography and flow regimes of each watershed (Magnuson et al. 2000; Austin and Colman 2007; Kaushal et al. 2010; Leppi et al. 2014; Lisi et al. 2015; Mauger et al. 2016). Site-specific physical characteristics thus act as climate filters that alter large-scale weather patterns and are predicted and observed to result in highly localized biological impacts (Bryant 2009; Griffiths et al. 2014; Turner et al. 2014; Whitney et al. 2016). Beyond site-specific climate effects in freshwater, species that move across ecosystem boundaries are likely to experience greater climatic and environmental variability (Hegemann et al. 2012; Dingle 2014) and thus be more susceptible to the impacts of climate change.

Anadromous Pacific salmon (*Oncorhynchus* spp.), which rely on both freshwater and marine ecosystems for their life history, are prime candidates for experiencing the wide effects of climate change (Thackeray et al. 2010; Lynch et al. 2016; Whitney et al. 2016). Pacific salmon populations have demonstrated the capacity to adapt to changing environmental conditions throughout their ranges and exhibit adaptive plasticity that promotes survival (Bryant 2009; Chen et al. 2016; Poesch et al. 2016). An archetypical life history of semelparous species of Pacific salmon incudes embryo incubation, hatching, a variable amount of time rearing (days to years) in freshwater, and a seaward migration to the ocean where the majority of somatic growth occurs before returning to natal streams to spawn and then die soon after (Groot and Margolis 1991; Quinn 2018). The timing of return to freshwater appears to represent adaptive strategies that increase the probability of encountering favorable environmental conditions, which in turn, increase survival and reproductive success (Hodgson and Quinn 2002; Portner and Peck 2010; Chiaramonte et al. 2016). These behavioral local adaptations are thus the product of selection that maximizes individual fitness (Bronmark et al. 2014; Chiaramonte et al. 2016). There can also be significant variation in selection acting on migration behavior between sexes, presumably reflecting differences in intra-specific competition on the spawning grounds (Portner and Peck 2010; Clark et al. 2014; Chiaramonte et al. 2016; Limburg et al. 2016). Site-specific responses to climate change are likely to influence timing of migrations (Crozier et al. 2008; Martins et al. 2012, Kovach et al. 2015). Thus, understanding how adult migrations are influenced by environmental conditions is profoundly important for being able to fully comprehend and predict impacts of a changing climatic environment on Pacific salmon.

Migrations of adult salmonids returning to spawn are influenced by stream flow conditions (Banks 1969), especially during times of peak or extreme low flow (Dahl et al. 2004). Upriver migrations have been observed beginning in July or August respective of environmental and local variation (Pravdin 1940; Godfrey 1965; Polum 2015). Normal in-river migration can be categorized into three sections: 1) an active upstream migratory phase, 2) a searching phase with upstream movement, and 3) a holding phase prior to spawning (Oakland et al. 2001). Coho Salmon (*Oncorhynchus kisutch*) that migrate upriver towards the beginning of the run, tend to travel farther upriver than fish that enter later in the season (Briggs 1953; Dahl et al. 2004). Optimal river conditions for Coho Salmon include high, well-oxygenated water levels (greater than 5.0 parts per million; Bhatnagar and Devi 2013), which increases available space for in-river movement, and cool water temperatures (8°C to 15°C) that maximize swimming ability and resistance against disease (Stenhouse et al. 2012). Trends towards elevated river temperatures and fluctuating local flow regimes might be expected to have a negative effect on salmon during the upstream migratory life history stage (Banks 1969; Quinn et al. 1997). Coho Salmon are vulnerable to low flow and warmer air temperature, which when combined, create stressful environmental conditions and lead to reduced stream carrying capacity (Smoker 1955; Sharma and Hilborn 2001). Like other species of migrating adult salmon, Coho Salmon may congregate around river mouths during poor flow conditions, holding for extended periods until suitable river conditions for upriver migration are present (Quinn 2018). These fish may initiate upstream movement excursions to evaluate river conditions and, in some cases, may even return to saltwater if conditions remain unsuitable (Raby et al. 2016). Migration during periods of low flow appears to be riskier relative to movement during periods of higher flow. Ellis (1962) found that during low water flow events, Coho Salmon were more vulnerable to predation by bears while moving through shallow riffles. Richard et al. (2013) reported that the reproductive success of Coho Salmon increased by later entry date and relatively cool river temperatures, perhaps reflecting reduced survival during low flows and warm water temperatures that occurred prior to fall freshets.

Extremely low or high flow conditions can restrict access to natal spawning sites during specific time periods thereby narrowing the spawning window for some populations. Briggs (1953) found that in higher latitudes, spawning Coho Salmon had earlier spawning timing. Site-specific temperature regimes of spawning habitat appear to shape this timing (Brannon 1987; Witteveen 1998). Spawning timing is thought to coincide with conditions that link temperature-dependent developmental rate and emergence timing, synchronizing with timing of suitable conditions in spring (Bams 1969; Brannon 1987).

Like many freshwater ecosystems in Alaska, the Buskin River on Kodiak Island, Alaska, is undergoing change. This system has a naturally flashy flow regime characterized by abrupt high-water events and low water periods (Stratton and Evans 2016). These high and low water events appear to have a large influence on migration and spawn timing. The Alaska Department of Fish and Game (ADF&G) has used a weir to monitor Buskin Coho Salmon escapements (i.e., the number individuals that survive fisheries and enter freshwater for spawning) since 1985. From 1985 to 2008, the weir was moved in mid-August from a location in the upper watershed at the outlet of Buskin Lake (7 km from mouth of river) and installed again at a lower location (approximately 0.8 km upstream from tidewater). In 2009, a second lower weir was added, and the two weirs were operated concurrently with one at the lake outlet and one in the lower watershed (Figure 1). Since 2009, all official Coho Salmon escapement data are collected from the lower weir site, but Coho Salmon are counted through the lake outlet weir to record the number of Coho Salmon entering Buskin Lake. In 1999 a sustainable escapement goal (SEG) of 6,000 to 9,000 fish was established in the Buskin River, this goal was updated to a biological escapement goal (BEG) of 3,200 to 7,200 fish in 2005 (Clark et al. 2006). The BEG was updated again in 2011 to represent the current goal of 4,700 to 9,600 fish (Sagalkin et al. 2013). Since 2009, sufficient numbers of Coho Salmon have returned to the Buskin River to satisfy the lower bound of the escapement goal annually while providing surplus for harvest. For the first time in 2015, and again in 2016, the Buskin River Coho Salmon escapement goal was not met; however, causes of the failed escapement are unknown. It was speculated at the time that reduced escapement could be associated with observed warm water temperatures in fresh and saltwater, low flow rate, and/or low dissolved oxygen in the river. A lack of information on the ecology of adult Coho Salmon in the Buskin River impeded understanding.

The overarching goal of this thesis was to illuminate the in-stream ecology of adult Coho Salmon in the Buskin River watershed. I sought to identify spawning locations and to understand the impacts of environmental factors on the in-river movements of adult Coho Salmon. Within the context of a changing environment, concurrent with the two lowest Coho Salmon escapements to the Buskin River, it is important to better understand what factors might be associated with this decline in returns. Currently, the only biological data available on Coho Salmon for this system are estimates of abundance (catch plus escapement) and basic size and age information from 1985 to present. This project will reveal where Coho Salmon are spawning in the river network and increases our understanding of how Buskin River Coho Salmon respond to changes in environmental variables in terms of migration timing and in river movement. The information presented in this thesis is a large step towards predicting how Coho Salmon in this important watershed may respond to a rapidly changing environment.

The objectives of my first chapter are to test the assumptions that fish that migrate Buskin Lake are tributary spawning fish and fish that never migrate to the lake when the weir operates are main stem spawning fish. I utilized an Alaska Department of Fish and Game Sport Fish weir to deploy radio tags to track fish movement and final locations throughout the watershed. By tracking tagged fish, I am able to 1) distinguish between main stem and tributary spawners and identify spawning locations in the tributaries and main stem, 2) determine differences in run timing, length, and stream life between main stem and tributary spawners, and 3) locate important areas used for holding prior to spawning.

The objective of my second chapter is to explore the relationships between large, intermediate, and local scale climate variables with migration timing and in river movement. I combined 33 years of Alaska Department of Fish and Game run timing data with three years of acoustic telemetry data. With this information I am able to determine 1) the extent of freshwater entrance timing change over time, 2) the relationships between different scaled climate variables and freshwater entrance timing, and 3) the influence of precipitation and temperature on in-stream movement, travel rates and use of holding habitats.

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Chapter 1 Quantifying run timing and spawning locations to assess potential stock structure and premature migration of Coho Salmon in a small Alaska Watershed[1]

Abstract

The return timing of anadromous salmonids to freshwater for reproduction is highly heritable, reflects local adaptation, and is often used to distinguish stocks for management and conservation. Although complex stock structure is most often associated with large watersheds that have extensive habitat diversity, even small drainages can produce multiple co-occurring stocks. This project assessed drivers of stock structure of Coho Salmon in a small coastal watershed on Kodiak, Alaska that supports vital subsistence and recreational fisheries and is currently managed as a single stock. We radio-tagged 348 adult Coho Salmon upon freshwater entry into the Buskin River during the 2015, 2016, and 2017 spawning seasons and tracked movements to spawning locations. Two general reproductive groups of Coho Salmon were identified: main stem and tributary spawners. Pooled across years, 54% (range 47% to 61%) of tagged fish spawned in the main stem river and 46% (range 39% to 53%) entered the upper watershed and never reentered the main stem and thus presumably spawned in small tributaries of the 1 km^2 headwater Buskin Lake. Despite distinct spatial differences in spawning locations, main stem and tributary spawners did not differ significantly in migration timing into freshwater (difference in run timing of main stem vs. tributary spawners was 0.5 days) nor length (mid-eye fork tail; main stem mean length = 624.5 mm, tributary mean length = 612.2 mm). Unexpectedly, we revealed that nearly 70% of all fish spent at least some time in the lake, including 54% of main stem spawners, suggesting a potential role of Buskin Lake as critical

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habitat for adult Coho Salmon who enter freshwater in advance of final maturation. We also identified areas consistently used for holding that during times of necessary conservation could be used for management based on spatial locations (closure or reduced bag limits) to ensure integrity of the stock for the future.

Introduction

The return timing to freshwater natal locations by anadromous salmonids for spawning can be extremely variable within and among species and is a hallmark of local adaptation (Hodgson and Quinn 2002, Quinn et al. 2016). Run timing of Pacific salmon is thought to be shaped by natural selection to increase the probability of individual survival and reproduction, and thus maximize fitness. Fitness may be maximized by synchronizing migratory timing to freshwaters, given local and regional temperature and flow regimes (Brannon 1987). This allows homeward migrating adults to reach spawning grounds and spawn at a time that facilitates a match between timing of juvenile emergence the following spring and availability of prey (Brannon 1987, Boatright et al. 2004, Quinn 2018). For example, populations and species that spawn in locations far inland or at high elevations tend to migrate earlier in the season than populations that spawn closer to the coast (Brannon et al. 2004, Hodgson and Quinn 2002, Quinn 2018, Neuneker et al. *in prep*). Similarly, species and populations spawning at higher latitudes typically spawn earlier than populations in more southern latitudes, consistent with the idea that relatively cool temperatures during incubation require more development time relative to warmer environments (Sandercock 1991). In addition to the ultimate fitness drivers for variable run timing, environmental and social interactions may serve to behaviorally cue the timing of entry to spawning grounds (Keefer et al. 2008, Anderson and Beer 2009, Berdahl et al. 2018). Compounding behavioral effects of run timing between spawning locations within the same system can influence sub-stock entry timing and stream life length (Burger et al. 1985, Clark et al. 2015).

Stock-specific run timing facilitates the evolution of partially reproductively isolated populations of Pacific salmon (Ricker 1972, Taylor 1991, Quinn and Dittman 1990, Quinn 2018) and thus contributes to the stock structure that defines management units. Differences in migration modes, spawning location, and timing can reduce competition among stocks or sub-stocks utilizing the same watershed leading to increased habitat capacity of a system (Burger et al. 1985, Boatright et al. 2004, Keefer et al. 2008). For example, Sockeye Salmon returning to Bear River, Russian River, and Chignik River in Alaska each have Sockeye Salmon stocks that return as early runs in June and July and late runs from July through September (Boatright et al. 2004, Eskelin and Barclay 2013, Chasco et al. 2007); these stocks have shown bimodal peaks of migration and spawn timing (Boatright et al. 2004) where different sub-populations spawn in distinct habitats with unique thermal regimes. Similarly, the Columbia River and Kenai River each have multiple distinct Chinook Salmon runs (early and late) documented to have separate spawning grounds, timing, and stream life duration (Burger et al. 1985, Keefer et al. 2008).

Populations within and among species may delay run and spawn timing (Quinn 2018). Quinn et al. (2016) described the phenomenon of adult salmonids entering freshwater in an immature state many weeks or months prior to spawning as 'premature migration'. Two non-mutually exclusive hypotheses exist that may explain premature migration in nature. Specifically, premature migration may occur when *i*) access to suitable breeding sites is constrained seasonally by barriers in flow or temperature or *ii*) the benefits of additional growth at sea are less than the potential risk of mortality in freshwater prior to spawning (Quinn et al. 2016). Premature migration might be expected to occur more often in populations that face the stresses of traveling long migration distances or metabolically taxing temperatures (Hawkins 1989). For example, Chinook Salmon spawning migrations in the Yukon River can span over 3,000 km starting from early May through mid-July; spawning occurs in late-July to early September (Mundy 1982). Rand et al. (2011) studied Sockeye Salmon migration on the Fraser River that migrated approximately 1,065 km in river, entering fresh water in early July spawning in mid-July to September. Similarly Sockeye Salmon in the Snake River migrate 1,444 km beginning in late June spawning in July and August (Keefer et al. 2008). These migrations create a situation where earlier freshwater entry timing may allow the fish greater flexibility to avoid sub-optimal river conditions experienced throughout the freshwater migration. Premature migration may also be more common in watersheds that have lakes or other habitat features that protect holding salmon from predators, stressful water environments, or inefficient energy consumption (Quinn et al. 2016). Despite these tenets, the current understanding of premature migration within and among populations is limited.

Much of what is known about prematurely migrating salmon has been provided from research in large river systems, presumably because extra time is needed to travel to the upper reaches of spawning grounds (Eiler et al. 2015, Quinn et al. 2016) and these systems provide suitable habitat for extended holding (Quinn et al. 2016). It follows that in shorter and smaller systems and in response to predation risks, fish that enter prematurely also need habitat that allows safe holding and stability until spawn timing arrives. Deep pools along rivers and lakes are an important refuge from predation (Nielsen et al. 1994, Gende et al. 2004). With the cessation of feeding once in freshwater, energy reserves are also a concern for premature migrating salmon; the lower flow rates of deep river sections require less effort for a fish to hold position (Anlauf-Dunn et al. 2014) allowing individuals to conserve energy for upriver migration and subsequent reproduction. Similarly, lakes that occur along salmon migratory pathways have been shown to provide safe holding areas for salmon to wait for advantageous conditions and to reach the spawning grounds (Newell and Quinn 2005). Thus, with the option to hold in a lake, salmon can adjust migratory and spawn timing to coincide with favorable environmental conditions. Within a population, individual fish may react differently to variables faced in terms of migration timing. Subsequently, safe holding areas give the potential for salmon to be adaptive to their local environment, shifting spawn timing and thus, life history patterns.

The majority of premature migration studies have studied Chinook Salmon, Atlantic Salmon, and Steelhead Trout, and other species have been shown to exhibit this phenomenon (Quinn et al. 2016, Reed et al. 2017). It is unknown if Coho Salmon exhibit premature migration; however, Coho Salmon may be a good candidate for which to investigate how premature migration may occur in smaller systems as they experience flow constraints and may avoid predation by arriving early and holding in a river main stem or lake until access to spawning grounds are available.

Knowledge of stock structure within a system is paramount for sustainable fisheries management such that harvest does not exhaust any one portion of the run. Harvested stocks can be described by fisheries managers as groups of fish exploited in a specific area that do not necessarily differ genetically (Smith et al. 1990), with long term management aiming to conserve intraspecific biodiversity (Coyle 1997). Variations in run timing by distinct stock components, such as with premature migration, can complicate management. For example, higher than average numbers of salmon returning earlier to fresh water may suggest a large run instead of an early return, while runs arriving later can appear as a smaller run (Walsworth and Schindler 2015, Adkison et al. 2015). Thus, stronger fishing pressure on one portion of a run could lead to stock overexploitation (Hodgson et al. 2006, Quinn et al. 2007, Adkison et al. 2015). Within small systems, the likelihood of in-river harvest is likely to increase with time spent in the river when a fishery is active. Understanding the life history patterns of specific stocks and within-stock structure is important for the optimal management of the resource.

In this paper we assess premature migration and the existence of stock structure in adult Coho Salmon migrating in a small coastal watershed on Kodiak Island, Alaska. The Buskin River provides an ideal case study to explore premature migration in smaller river systems because of its size, ability to easily access the majority of the watershed for tracking individuals, and possible presence of multiple spawning groups. It has long been assumed that fish that migrated into the headwater lake were spawning in lake tributaries and fish that never migrated to the lake spawned in the main stem, resulting in the potential spatial separation of two spawning groups (D. Tracy, ADFG, Kodiak, personal communication). We test this assumption through the following objectives: 1) identify spawning locations in the watershed and distinguish between main stem and tributary spawners, 2) quantify differences in run timing, length, and stream life between main stem and tributary spawners, and 3) identify important areas used for holding prior to spawning. We expect that two distinct spawning groups will emerge, and fish will primarily use several known deep pools in the river and the lake at the head of the system as holding habitat.

Methods

Study Area

The Buskin River watershed (67 km^2) adjacent to the city of Kodiak Alaska, on Kodiak Island (Figure 1) produces vibrant and important subsistence and sport salmon fisheries. The main stem of the river is approximately 5 km long, drains from Buskin Lake (surface area: 1.0 x 10^6 m^2 and average depth: 18.9 m; ADFG 2018), and is fed by five tributaries that drain into Buskin Lake (Pacific and Pelagic 2004). The Buskin River watershed experiences a temperate marine climate with an average autumn (August-November) precipitation of 180 mm, and an average autumn daily water temperature of 10°C (National Oceanic and Atmospheric Administration Weather https://www.ncdc.noaa.gov/cdo-web/datasets#GHCND). Anadromous adult salmon returning to this system can access a total of approximately 10 km of the river and tributaries for upriver migration and spawning, which contrasts with salmon returning to large rivers such as the Yukon (3,200 km; Eiler et al. 2015), Susitna (400 km; Yanusz et al. 2013), or Columbia (2,000 km; Keefer et al. 2008).

Tagging and Tracking

Coho Salmon enter the Buskin River over a protracted period between August and October with a median 50% run date (date which 50% of the run occurs prior to) of September 15 (Stratton and Evans 2017). Returns of Coho Salmon to the system have been monitored by the Alaska Department of Fish and Game (ADF&G) by weir count estimates since 1985. A lower weir is located 0.8 km from the mouth of the river and an upper weir at the outlet of Buskin Lake is located 4.6 km from the mouth (Figure 2). An additional weir is located on the tributary from the Lake Louise drainage, 0.25 km above the lower weir, between June 1 through September 15 (Figure 1). There are three deep, slow moving sections of river that are thought to provide potential refuge for fish migrating upriver and are well known locations for sport fishing (Figure 1).

The Buskin River Coho Salmon run has an average estimated escapement (i.e., the number of fish entering the river to spawn that have survived ocean fisheries and natural mortality at sea) of 6,107 fish during the period 2008-2017 with a maximum weir count of 10,624 fish in 2009 and a minimum of 2,513 fish in 2016 (Stratton and Evans *in prep*). This run is enumerated at the lower weir, and again when entering the lake in an attempt to capture escapement of Coho Salmon utilizing the upper watershed, and presumably, the tributaries of the lake for spawning (Table 1). The lower Buskin River weir is highly susceptible to high water events that make counting fish passage difficult and sometimes impossible at the highest flows. During 2016 and 2017, the lower weir was frequently inundated with turbid water and reinstallation was necessary.

Identifying spawning locations and distinguishing main stem vs. tributary spawners

Using the combination of mobile and fixed telemetry listening stations, we assigned the designation of 'tributary spawners' to individuals from which we received mortality signals from above the lake weir, and 'mainstem spawners' to individuals that were detected dead below the lake weir. Post season, raw tracking station data were organized by individual tag frequency and combined with mobile surveys to construct the weekly location of each fish throughout the season. Lake entrance (day of year [DOY] fish passed lake weir) was determined when the signal strength of the upstream antenna was stronger than the downstream antenna and was never again opposite (which would indicate downstream movement out of the lake). We used similar logic to assign DOY of lake exit (when downstream signal was stronger than upstream signal). Extent of stream life was calculated as the difference in days between tagging upon freshwater entrance and first day of recorded mortality signal.

Holding Areas

Holding areas, defined by fish spending at minimum of two consecutive days in a location, were identified by plotting mobile detections by river section with the goal of visually identifying hotspots. Detections from mobile surveys were organized by river section for the months of August, September, October and November. The total number of monthly detections were mapped for each reach across 2015, 2016, and 2017 in ArcGIS software (ESRI version 10.5).

Statistical Analysis

Differences in run timing, length, sex composition, and stream residence time between main stem and tributary spawners

We used tag date as a proxy for freshwater run timing. For mainstem spawners, lake residence time was determined by subtracting the DOY of lake entrance from the DOY of lake exit, and for tributary spawners DOY of lake entrance from DOY of mortality. For both mainstem and tributary spawners, we calculated stream life as the difference between DOY tagged entering the river at the lower weir and the DOY to final location.

To test the hypothesis that main stem and tributary fish were different in a suite of traits that often characterize stock structure, a subset of eight generalized linear models was created using the Program R (www.r-project.org) package AICcmodavg (Mazerolle 2019) to identify variables that best explained the variation in spawning location given the data. Specifically, the response variable was mainstem or tributary spawning (coded as 1,0) and the predictor variables were fixed effects of tag date (DOY), sex (male, female), and body length (MEFT, mm) of Coho Salmon passing the Buskin River lower weir. Following Burnham and Anderson (2002), we then the most parsimonious model was identified based on the lowest delta AICc and highest cumulative Akaike weight, but also considered other models within four delta AICc units to have substantial weight of evidence. We used t-tests to assess the hypotheses that mainstem and tributary spawners differed in *i*) the number of days alive in the river (i.e. stream life) and *ii*) number of days to travel to final spawning locations. Similarly, we used a t-test to test the hypothesis that fish that died prematurely compared to fish with assigned final spawning locations entered the river at different times.

Results

Identifying spawning locations and distinguishing main stem vs. tributary spawners

We tagged 348 adult Coho Salmon (Table 2) that entered the Buskin River across three spawning runs: 2015 (n = 92), 2016 (n = 96), and 2017 (n = 160). Of these tagged Coho Salmon, we received mortality signals and were able to assign 235 fish to a final spawning location (Table 3). The 235 fish that were assigned final locations were composed of 105 females and 130 males. The river main stem had 127 Coho Salmon spawners (2015 n = 34, 2016 n = 46, 2017 n = 41; Table 2) over the three-year period while the upper tributaries had 108 Coho Salmon spawners (2015 n = 46, 2016 n = 30, 2017 n = 33; Table 2). The average tag deployment date over the three years was September 15 (mean DOY = 257, SD = 10.7; Figure 2). In 2015, extreme low water conditions delayed Coho Salmon entrance timing. Despite substantial effort, no radio tag signals were received on stationary towers except for at the lake weir and Buskin Lake stations.

Differences in run timing, length, sex composition, and stream life between main stem and tributary spawners

Model selection revealed very weak evidence that tributary and main stem spawning Coho Salmon differed in run timing (mean average difference in DOY of river entry was 0.5 days; Figure 3), proportion of males or females (mainstem = 52%, tributary = 58% male), or body size (mainstem average length = 625 mm, SD = 49.3 vs. tributary spawners average length = 612 mm, SD = 52.2). The best model selected was length alone (AICc = 325.03, Delta_AICc =

0.00, AICcWT = 0.32), while the full model included tag date, sex, and length did not rank highly (AICc = 328.6, Delta_AICc = 3.11, AICcWT = 0.07).

The remaining 113 radio tagged Coho Salmon had undetermined fates which we interpreted as being caught by sport fishermen, defective tags (unlikely given tags are tested just prior to deployment) or eaten by predators (most likely coastal brown bears *Ursus arctos*) and moved out of range of our surveys

Overall, Coho Salmon spent a mean of 52 days in the Buskin River watershed (range 19-95 days, SD = 15.7). Tributary spawning fish spent significantly longer (an additional 10 days) in the watershed than fish that spawned in the main stem river (t = 4.8, df = 230, p-value = <0.0001). Tributary spawners took an average of 29 days (SD=19) to travel to their final location (determined by the first date a tag was detected in an area before detecting a mortality signal), while residing 57 days on average (range 39 to 95 days, SD=12.8) in the Buskin River watershed. Main stem spawning Coho Salmon also took an average of 29 days (SD = 18.5) to travel to their destination but resided an average of 47 days (range 19 to 88 days, SD = 16.8) in the river.

Although main stem and tributary spawners did not differ in run timing, the mean date of entrance of individuals inferred to have died prematurely was September 11 (254 DOY, SD = 7.7), which is 4 days earlier than fish which likely died natural deaths following spawning or attempting to spawn (p-value = <.001). However, prespawning mortalities and those with known fates did not differ significantly in mean length 623 mm (SD = 45.8); the average tagged Coho Salmon in the Buskin River watershed was 620 mm (t = -0.412, df=202.7, p-value = 0.681; Figure 3)

Holding Areas

As predicted, tagged fish were generally located in sections of the river categorized by relatively deep, slow water also identifiable by popular Coho Salmon fishing locations along the river (popularly known as Pumphouse Hole, Island Hole, Beaver Pond) and in the lake (Figure 1; Table 5). As the day of year progressed, 70% of tagged fish advanced into the lake, while the remaining tagged fish remained in the main stem and never enter the lake. The distribution of tagged fish in August throughout the watershed looked similar in 2015 and 2016, with no tags being deployed in the river at that time in 2017. By the end of August in 2016, only 3 fish had migrated past the Pumphouse Hole. In 2016 and 2017, more substantial amounts of rain had fallen than in 2015 in total, and the number of tagged fish that migrated up stream was greater in September and October. Counter to previous assumptions, both tributary spawning fish and river spawning fish utilized the lake (N = 162 fish). Of the 162 tagged fish that spent time holding in the lake, 42% dropped back down to spawn in the main stem of the river after the lower weir was pulled (September 30). Of the 108 tributary spawning fish, 49 tagged fish spent 10 or more days holding in the main stem of the river before entering the lake and continuing on to the tributaries. A Welch two sample t-test showed main stem-spawning Coho Salmon spent less time holding in Buskin Lake (mean = 14 days, SD = 9.6) relative to tributary-spawning fish (mean = 29 days, SD = 9.2; t = 7.6, df = 65.6, p-value = 1.346e-10).

Discussion

We quantified the potential for stock structure in a small coastal watershed by identifying spawning locations to run timing and other traits associated with distinct population segments used in management. Four salient results emerged from this work. First, we distinguished two general groups based on spawning location; one group spawned in main stem areas and the other in tributaries in the upper watershed. Second, despite spawning in different locations, main stem and tributary spawners did not differ in migration timing, sex ratios, or length, consistent with the interpretation of a single stock structure. Third, although fish migrated at the same general time, fish that spawned in tributaries averaged 9 days longer between freshwater entry and post-spawning mortality compared to main stem fish, which may reflect an adaptation to variable stream flows in small tributaries that makes access unpredictable (Newell and Quinn 2005). Fourth, we identified important deep pool and lake holding habitats that were consistently used across all three years; some of these areas may put fish at greater risk of harvest. Taken as a whole, the use of radio telemetry revealed potential spawning population structure of Buskin River Coho Salmon and simultaneously indicated that main stem and tributary spawners likely experience similar vulnerability to fishing pressure, both in the near shore subsistence fishery and the sport fishery given large overlap of migration timing.

Similar to other studies (Eiler et al. 2015; Quinn et al. 2016), it does not appear that the entire population of Buskin River Coho Salmon migrate prematurely to the watershed. However, individuals utilize areas of stable habitat in response to environmental stressors (Sherer 1990). The average stream life for a Buskin River Coho Salmon was 52 days ranging from 19 to 95 days. Van den Bergehe et al. 1986 found that Deer Creek Coho Salmon in Washington State, stream life was 9 days, ranging from 3 to 17 days. Most Chum and Pink Salmon enter rivers at an advanced maturity state and spawn within 30 days of entry (Quinn et al. 2016). In Auke Creek, Fukushima et al. 1997 found that Pink Salmon stream life ranged from 5 to 10 days, averaging 7 days. Quinn et al. (2016) found that although many explanations for premature migration existed, most models included a tradeoff for growth at sea. The incremental fitness benefit of staying in the ocean for longer may not be as strong for Buskin River Coho Salmon (average length 620 mm). Whether main stem and tributary spawners are sufficiently isolated in space to result in being genetically different stocks is worthy of future investigation. The consistent use of Buskin Lake by both main stem and tributary spawners has important management applications which we discuss below.

Past studies on river systems larger than the Buskin River have shown a tendency for salmon that return earlier to natal streams to travel greater distances to spawn (Burger et al. 1985, Clark et al. 2015, Eiler et al. 2015, Neuneker et al. *in review*). In general, Coho Salmon spawning migration timing takes place in the late fall (Sandercock 1991, Quinn 2018). Tag date, used as a proxy for entrance timing, did not distinguish whether a Coho Salmon entering the Buskin River would migrate to the upper tributaries or remain in the main stem, counter to the general assumption that earlier arriving fish travel farther (Brannon et al. 2004, Hodgson and Quinn 2002, Quinn 2018, Neuneker et al. *in review*). It seems likely given the small size of the Buskin River watershed, where we observed the entire migration from lower weir to the lake in the upper watershed easily accomplished by two individuals in a single day, the advantage of arriving early is much lower than on larger rivers that use this time to migrate a much greater number of kilometers. Sockeye Salmon from the Snake River take an average of 47 days to complete their migration of approximately 1,400 km (Crozier et al. 2014), while the average travel time to Buskin Lake was 17 days (SD=14.6). However, early arrival may allow additional time for Buskin Coho Salmon to encounter optimal water conditions for holding if the environmental factors preclude smaller tributary access.

Although entrance timing was not associated with migration distance for Buskin Coho Salmon, we observed substantial variation in the amount of time fish spent in the watershed. In general, Quinn et al. (2016) defined premature migration as entering freshwater greater than 3 months in advance of spawning; however, their results were constrained to studies where river length ranged from 45 km to 3,000 km. In a system that is 10 km long, and migration can be completed within a single day, “premature migration” could look different. Freshwater migration for Sockeye Salmon in the Snake River averaged approximately 30 km of upriver movement a day (Crozier et al. 2014) while Buskin River Coho Salmon averaged around 0.6 km per day. This difference in travel rates shows the overall importance of available holding habitat. Over the three years of this study, Coho Salmon spent between 19 and 95 days in the watershed and arrived, on average, 52 days before natural death following spawning. This period of holding prior to spawning emphasizes the importance that less energetically taxing, stable habitats (not subject to drastic water level or flow rates) be available to migrating individuals, regardless of the travel distance. The average tributary spawning fish spent 9 days longer within the watershed than main stem spawning Coho Salmon, which was a significant difference between the two groups. Both groups of fish had similar mortality time frames with the exception of 2015 when mortality signals for main stem spawners were earlier than tributary spawners. This difference, which is indicative of the tributary fish holding longer in the lake prior to spawning, may be because of genetic differences between both groups, environmental cues, or it could be spurious and reflect an anomalous year. Notably, in 2015 when river flow was unusually low, 59% of the tagged fish entered Buskin Lake, compared to 34% and 44% for 2016 and 2017, respectively, when flow conditions were generally improved. The observation that Coho Salmon did not enter Buskin Lake tributaries shortly after entering the lake suggests that environmental constraints within upper tributaries of the Buskin watershed forced Coho Salmon to hold in the lake until conditions improved (Anlauf-Dunn et al. 2014). Although we did not directly assess energy density of adult Coho Salmon, extended stream life is unlikely to be explained by differences in fat or lipid reserves as tributary and main stem spawners did not differ significantly in length despite that smaller fish likely have an advantage accessing shallow spawning grounds (Quinn et al. 2007b, Doctor et al. 2010). It is likely that the nine extra days of stream life observed in tributary spawners could be an adaptation to potentially unpredictable environmental conditions that affect access to spawning grounds and the ubiquitous need to conserve energy for spawning after entering freshwater by holding in stable habitats (Quinn et al. 2016).

Although we found no significant differences in migration timing between main stem and tributary spawners, our results suggest potentially higher mortality for fish that enter the river earlier in the season. Fish that were harvested by anglers or died prematurely, arrived on average 4 days earlier than fish that did not die prematurely. Consistent with this finding, angler fishing effort on the Buskin River is higher during August and early September and tapers off in October (Stratton and Evans 2017), which coincided with tags being deployed and a decrease in the daily harvest limit of Coho Salmon from two to one fish after September 16, 2017. Sport fishing Coho Salmon creel surveys for ADF&G end the final week of September due to drastically decreased angler encounters on the river, reflecting shifts in effort. Buskin Coho Salmon are, on average, comparable in size to other stocks located on Kodiak Island (Wattum 2017), suggesting they have might have less benefit for staying longer at sea. Undetermined fate fish, including sport-caught tagged fish had slightly larger length than tagged fish that did not have undetermined fates suggesting early season sport fishing selectivity could play a role in this difference (Table 1). The small size of the river combined with its proximity to the City of Kodiak, concentrates fishing pressure more than in a larger river system, with 80% of the fishing pressure taking place in the 0.8 km below the lower weir (Murray 1987). In 2015, a large portion of the Buskin River Coho Salmon run was harvested in the sport (73%) and subsistence (13%) fisheries (Table 1) likely due to the drastically limited migration movement in the river. Fish were forced to hold in the lower river and near shore estuary for an unprecedented time period, which also parallels the area of heaviest fishing pressure. In 2016, the river had consistent water levels throughout the season and concurrent closures to both fisheries resulted in unobstructed passage and allowed fish to migrate on their own timeline, which lead to smaller harvest numbers (sport fish=39%, subsistence=10%). The final year of the study saw both passable water levels in the river for migration and the introduction of a new harvest regulation reducing the bag limit of Coho Salmon to 1 after September 15. The harvest rates reflected this change and had the lowest reported harvests of the study (sport fish harvest 29%). Thus, fishing selectivity could affect our ability to randomly assess the entire population as we could only tag fish that avoided harvest below the lower weir. Although no bear-killed Coho Salmon were directly observed, bears were seen fishing on many occasions and seems a likely fate for an unknown fraction of the 113 tags that do not have final mortality locations assigned to them. Also, tag failure could be a possible explanation for a portion of tags that had an undetermined fate, but we think this is highly unlikely as all tags were confirmed to be functioning when deployed.

We identified Buskin Lake and three large, deep pools as potential critical habitat for migrating adult Coho Salmon. Both main stem and tributary spawning groups of Coho Salmon utilized these habitats. It has been shown that adult Chinook Salmon and summer Steelhead Trout hold in the deepest available pools within a river (Nakamoto 1994, Brannon et al. 2004, Anderson and Beer 2009, Quinn et al. 2016), and larger pools provide more protection than smaller pools (Freese 1982). Atlantic Salmon have also been documented to utilize lakes for holding when migrating (Quinn et al. 2016; Reed et al. 2017). Although the fraction of fish that used deep pools and Buskin Lake varied among years, the locations where fish held remained consistent. This implies that stable geomorphic features of the river translate into predictable areas for holding (Jorgensen et al. 2009). The lake can provide sanctuary for fish that escape the sport fishing pressure and predator threats of the main stem before spawning conditions are realized. Consistent with the wide use of the lake, 42% of fish that migrated to the lake returned to the main stem for their final location post September 30, coinciding with the lake weir being pulled and decreased fishing effort. However, main stem spawners spent less time holding in the lake than tributary spawners. Brown (2005) tracked radio tagged Chum Salmon in the Kashunuk River and found that many fish that spent time in the river main stem were not engaged in active migrating behaviors but instead employed holding behavior. Buskin River Coho Salmon holding habitat areas aligned with well-known areas of higher sport fishing efforts. Such behavior could present a challenge to a Coho Salmon that has found suitable holding grounds through an increased likelihood of being harvested in the sport fishery, if a long period of time is spent in these sections.

In light of the similiarities in migration timing, length, and sex, and the fact that fish entering freshwater are generally not fully sexually mature, Buskin River Coho Salmon do not entirely meet the definitions for premature migrants as outlined by Quinn et al. (2016). However, it does appear that Buskin River fish utilize refuges in the form of Buskin Lake or deep holding pools in the main stem of the river prior to spawning for extended periods of time; although the migration distance is relatively short, it does present similar stresses to migratory fish. Similarly, the stock structure of the population, identified as tributary and main stem spawners, reflects how subpopulations may react differently to habitat conditions, as tributary spawners had a longer freshwater residence time than main stem spawners.

Conclusions and Management Applications

Prior to this study, Buskin River Coho Salmon that migrated through the Buskin Lake weir and into the upper watershed were assumed to spawn in lake tributaries and never reenter the main stem river, while fish that never passed the Buskin Lake weir were believed to spawn in the main stem. Our results provide clear evidence that *both* tributary and main stem spawning groups were documented in the upper watershed and used Buskin Lake prior to spawning. Indeed, radio telemetry identified fish movements continuing after the Buskin Lake weir was removed, refuting the assumption that only tributary spawners use the lake while also questioning the utility of the weir to accurately assess upper watershed escapement. Further use of the Buskin Lake weir for enumerating Coho Salmon is likely unnecessary due to the use of Buskin Lake as holding habitat for both main stem and tributary spawning fish.

We identified two spatially distinct spawning Coho Salmon groups that comigrate in time. Given this life history, it is unlikely that any group will be overexploited if harvest rates vary throughout the season. In other systems the harvest rate can differ markedly from the start to the end of the run, and to the extent to which populations segregate during migration may be exploited disproportionately if they come late or early in the run. In the Buskin River, the pattern of angler effort in low water conditions likely results in higher exploitation rates for early arriving fish. Indeed, we observed that earlier returning fish were more likely to die prematurely than fish that returned later. Despite this, the overlap in run timing between tributary and mainstem spawners provides a buffer against population-specific harvest. Current management and protection of habitat is likely to be maintaining the diversity of the main stem and tributary spawning cohorts within the Buskin Watershed.

We detected that some Coho Salmon in the Buskin River enter freshwater approximately three months prior to spawning events and utilize the deeper main stem pools and lake habitat as refuge. Murray (1987) determined that 20% of the sport fish harvest takes place above the lower weir. This means that when evaluating the weir counts, the escapement number would be estimated at 20% lower than the total weir counts. There are current regulations utilizing temporal management of this stock, but spatial closures above the lower weir to protect fish in identified holding habitats may be an option for ensuring adequate spawner abundance in times of conservation concern given the stability of locations of holding habitat. Closures above the lower weir may be possible to reduce harvest in Buskin Lake, Beaver Pond, Island Hole, and Pumphouse in times of conservation. Current tools the managers have to achieve escapement goals include changing the daily Coho Salmon sport fish bag limit and adjusting the subsistence fishing to match the necessary harvest levels. Spatial management options would necessitate a ruling by the Board of Fisheries.

Lakes are an underappreciated rearing habitat for salmonids (reviewed by Arostegui and Quinn 2019) and our results suggest lakes in Alaska or beyond may be critical for holding salmon prior to spawning. Indeed, observations from the Pacific Northwest corroborate the importance of lakes as thermal refuges for species such as sockeye salmon (Newell and Quinn 2005). Kodiak Island alone has multiple small coastal rivers with associated lakes that may be used similarly to Buskin River Coho Salmon and future work to explore the use of lakes by adult Coho Salmon would be illuminating. With the changing climate, the availability of thermal refuges will continue to be important for migrating fish in freshwater.

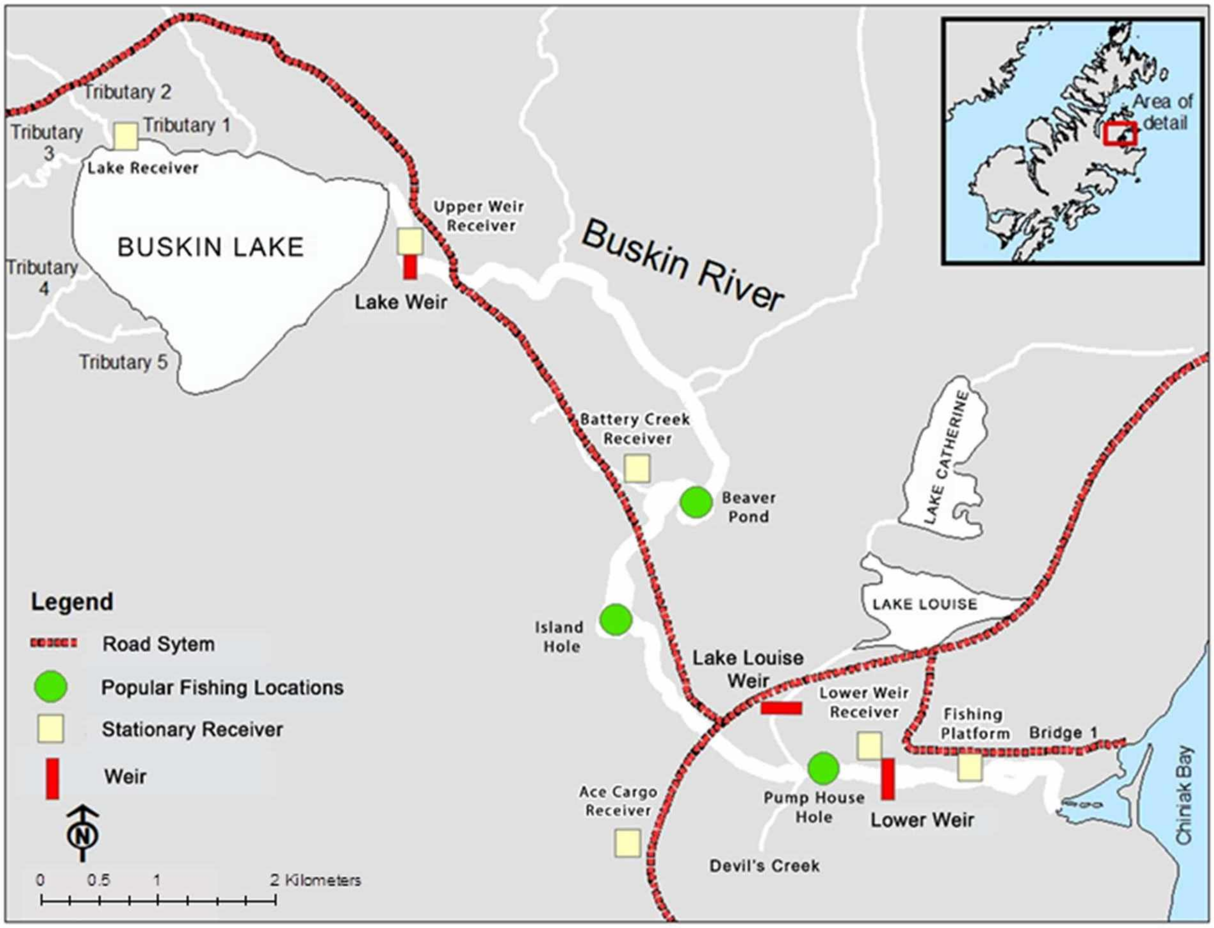


FIGURE 1.1 Map of the Buskin River watershed, Kodiak, Alaska (57 °46'N, 152 °32'W), showing the main stem river, lake and upper tributaries, weir locations, and tracking stations.

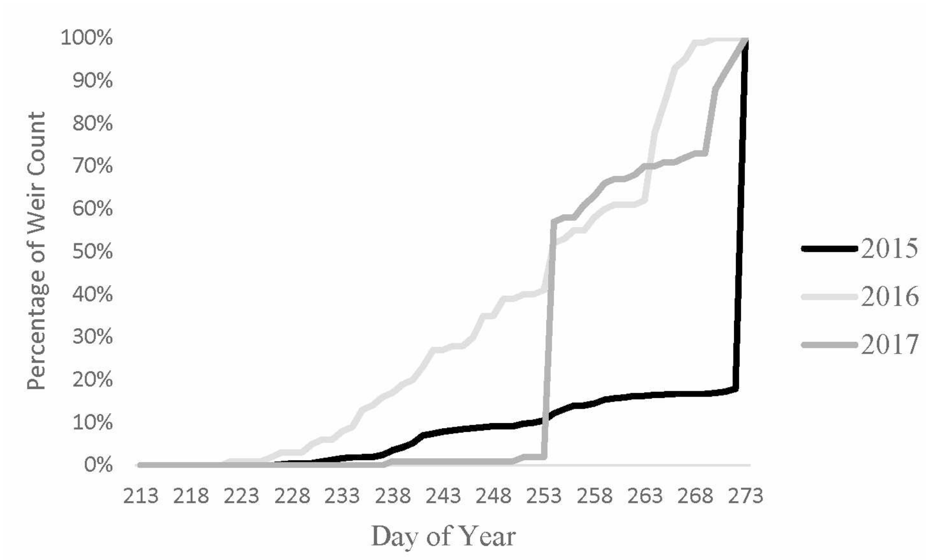


FIGURE 1.2 Cumulative proportion of Buskin River Coho Salmon weir counts in 2015, 2016, and 2017.

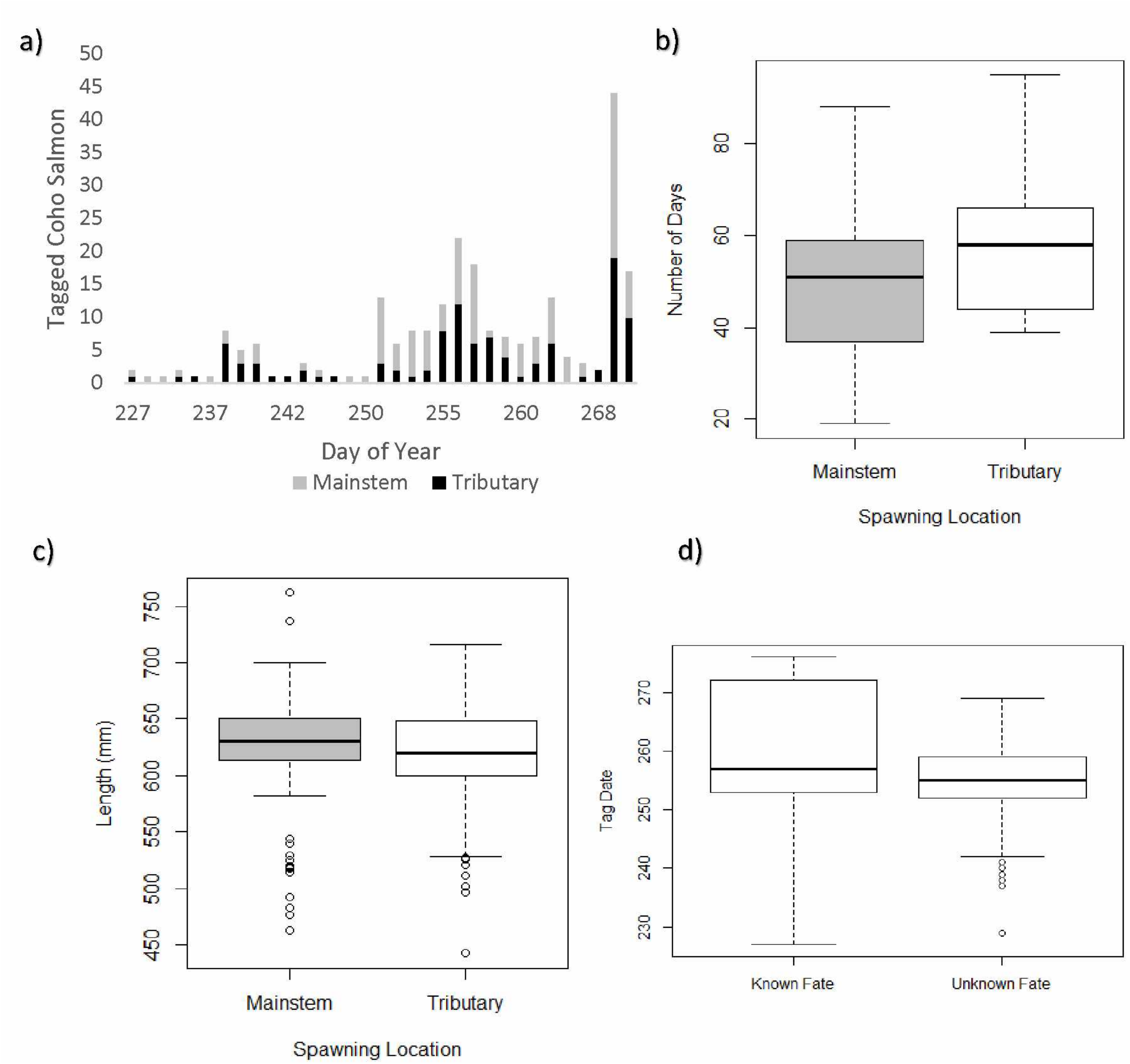
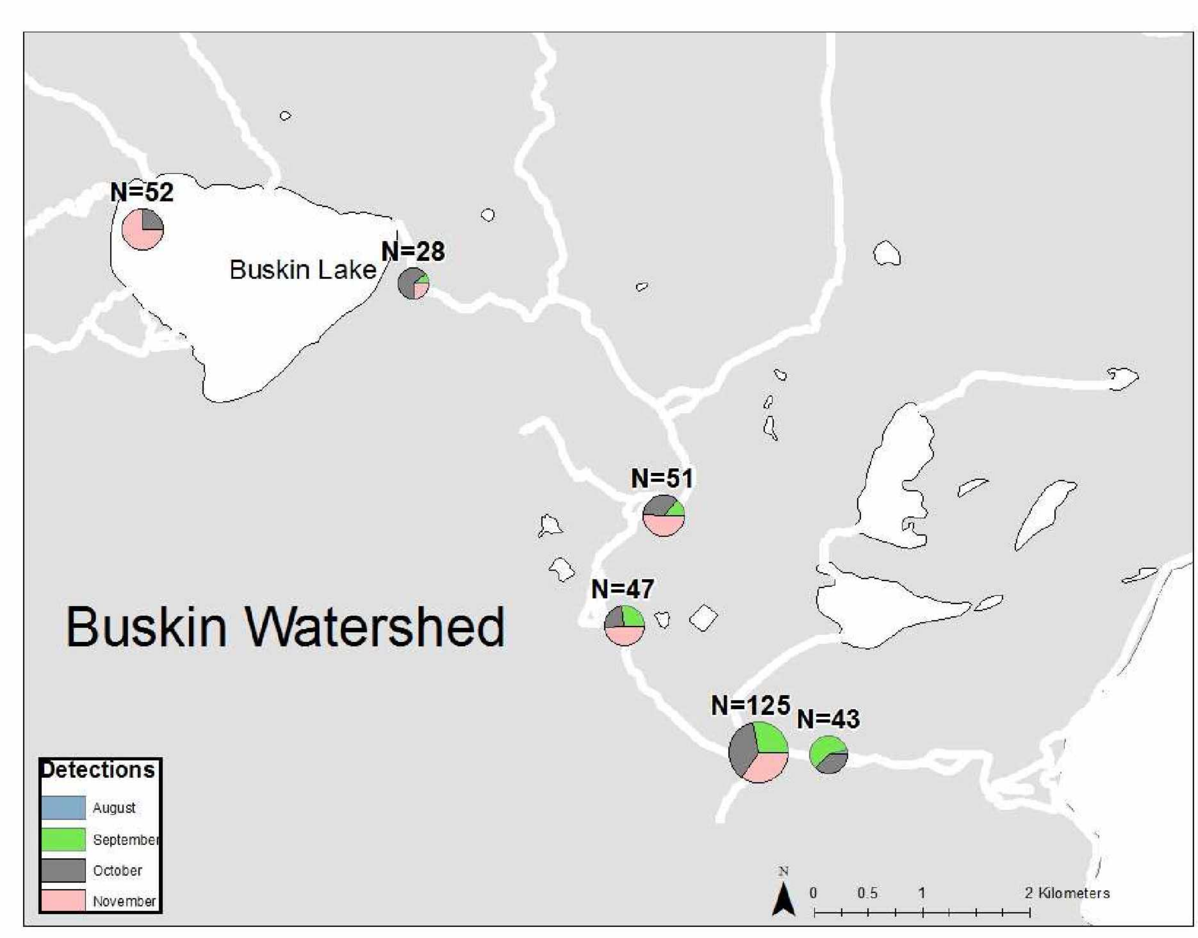
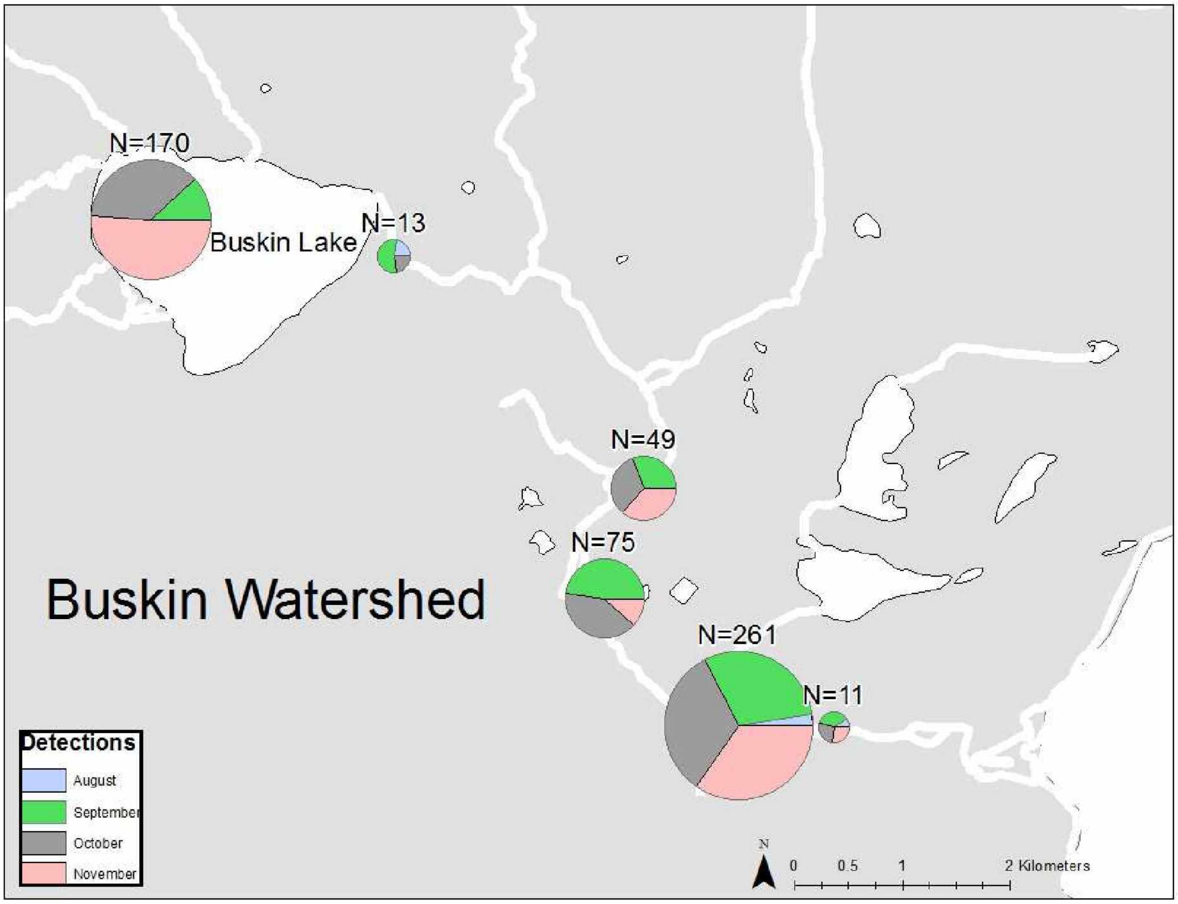


FIGURE 1.3 Mainstem and tributary spawners a) tag dates b) stream life, c) length, and d) premature mortality costs for 2015, 2016, and 2017.

a) 2015


N=52
Buskin Lake
N=28
N=51
N=47
Buskin Watershed
N=125
N=43
Detections
August
September
October
November
N
0
0.5
1
2 Kilometers

b) 2016



N=170
Buskin Lake
N=13
N=49
N=75
Buskin Watershed
N=261
N=11
Detections
August
September
October
November
N
0
0.5
1
2 Kilometers

c) 2017

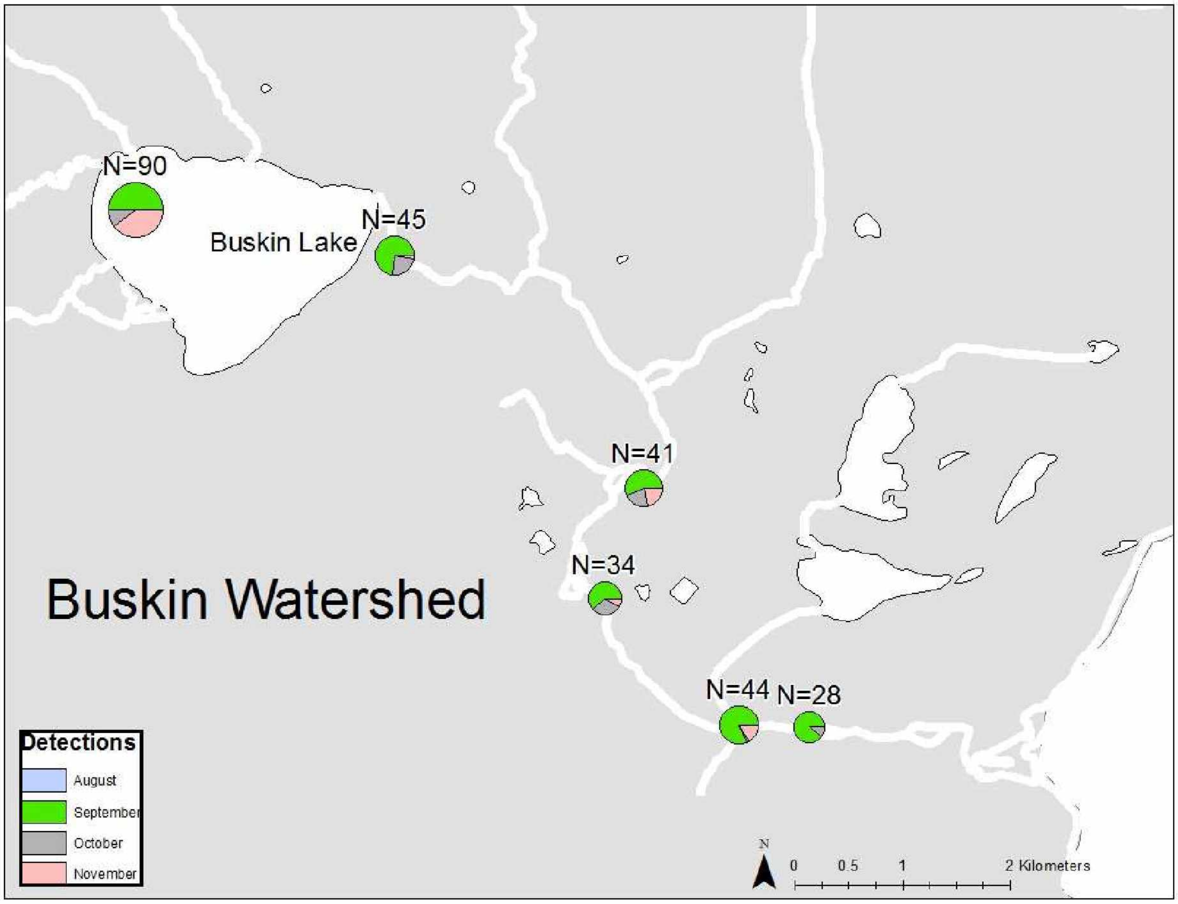


FIGURE 1.4 Map of the proportion of tagged Coho Salmon detections throughout the Buskin River watershed, Kodiak Island, Alaska during August (blue), September(green), October (grey), and November (pink) for a) 2015, b) 2016, and c) 2017.

TABLE 1.1 Buskin River lower weir count (% of total run), sport fish (SF) harvest (% of total run), subsistence harvest (% of total run) and total run (sum of weir count, SF, and Sub harvest) in 2015, 2016, and 2017.

Year	Weir count	SF harvest	Sub harvest	Total run
2015	904 (14%)	4,889 (73%)	884 (13%)	6,677
2016	2,488 (51%)	1,895 (39%)	496 (10%)	4,879
2017	5,559 (68%)	2,337 (29%)	300 (4%)	8,196

TABLE 1.2 Summary of radio tagged Coho Salmon sampled in 2015, 2016, and 2017, numbers of fish utilizing the lake, dropping back down to the main stem, locations of mortality signal locations, and undermined fate tags.

Category	2015	2016	2017	All years
Start of tagging	230	227	237	-
End of tagging	276	267	268	-
Tagged	92	96	160	348
% male	63%	52%	45%	53%
% female	37%	48%	55%	47%
Average length (mm)	611	632	618	620
Tags into lake	54	37	71	162
Tags exit lake	35	13	20	68
# Tributary Spawners	45	30	33	108
# Main stem spawners	40	46	41	127
# Undetermined fate	7	20	86	113

TABLE 1.3 Summary statistics for 2015, 2016, and 2017 tributary- and main stem-spawning tagged Coho Salmon.

	2015		2016		2017	
Location		SD		SD		SD
Tributary						
Number of spawners	46		30		33	
Average length (mm)	606	50.2	631	43.7	610	58.3
Average tag date (DOY)	266	11.8	252	10.2	253	8.4
Average lake entrance (DOY)	283	5.7	300	11.7	261	12.1
Average death date (DOY)	316	0	317	3.4	306	0.5
Average lake residence (days)	33	5.7	17	12.5	15	13.8
Average days to spawning location	22	16	25	18.1	35	22.3
Stream life (days)	50	11.8	64	10.6	55	8.7
Main stem						
Number of spawners	34		46		41	
Average length (mm)	619	52.1	639	35.8	621	43.6
Average tag date (DOY)	268	10.1	256	9.7	255	7.2
Average death date (DOY)	296	3.3	318	3.5	306	0.5
Average lake entrance (DOY)	282	3.3	297	6.9	262	8.7
Average lake residence (days)	15	9.8	21	10.5	16	10.4
Average days to spawning location	24	13.7	30	16	34	22.1
Stream life (days)	28	10.4	63	10.3	52	8.1

TABLE 1.4 Model selection based on Second-order Akaike Information Criterion (AICc) of Buskin River Coho Salmon spawn location variation using tag date (DOY), sex, and length (mm) variables. Number of parameters in model (K).

Model	K	AICc	Delta_AICc	AICcWt
Length	2	325.03	0	0.3181
Length+sex	3	326.348	1.3185	0.1645
Null	1	326.566	1.5356	0.1476
Tag date+length	3	326.785	1.7549	0.1323
Sex	2	327.65	2.62	0.0858
Tag date+length+sex	4	328.141	3.1112	0.0671
Tag date	2	328.592	3.5619	0.0536
Tag date+sex	3	329.694	4.6637	0.0309

TABLE 1.5 Total monthly detections of radio-tagged Coho Salmon in the Buskin River watershed based on mobile surveys for 2015, 2016, and 2017.

Location	August	September	October	November
Lower Weir	23% (3)	13% (54)	7% (22)	1% (3)
Pumphouse Hole	53% (7)	34% (145)	35% (128)	34% (134)
Island Hole	0% (0)	17% (70)	14% (51)	9% (35)
Beaver Pond	0% (0)	11% (45)	12% (45)	13% (53)
Lake Weir	23% (3)	10% (43)	9% (32)	2% (8)
Buskin Lake	0% (0)	15% (65)	23% (85)	41% (162)

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Chapter 2 Ocean and freshwater drivers influence timing of river entry and patterns of in-stream movement of Coho Salmon (*Oncorhynchus kisutch)* in the Buskin River, Alaska[2]

Abstract

The timing of freshwater entry by adult anadromous salmonids is both heritable and influenced by environmental factors. Migrating fish experience environmental factors operating at multiple spatial scales at different stages of their homeward journey: large scale ocean factors, conditions in the nearshore, and freshwater drivers during migration and spawning. To elucidate the role of environmental forcing on adult migration we combined 33 years of Buskin River Coho Salmon weir counts from 1985 to 2018 with three seasons of telemetry tracking (2015-2017). We quantified the influence of the Pacific Decadal Oscillation (PDO), sea surface temperatures (SST), local precipitation, and air temperature on timing of freshwater entry as indicated by the day of year when 10%, 50%, and 90% of fish had entered the river. We investigated precipitation and temperature effects on weekly travel distance (km), arrival at spawning locations, and residence time in Buskin Lake, which is a known habitat used by prespawning individuals. Unlike recent reports of shifting phenology in other species and regions, Buskin River Coho Salmon freshwater entrance timing date has not trended significantly earlier or later but is highly variable among years. Timing of 50% entry varied from DOY 243 (August 31) to DOY 272 (September 29) and 24% of that variation was explained with the combination of SST measured approximately 6 km from the river mouth, PDO, August

[2] Stratton, M. E., H. Finkle, J. A. Falke, and P. A. H. Westley. *In prep for North American Journal of Fisheries Management.* Ocean and freshwater drivers influence timing of river entry and patterns of in-stream movement of coho salmon (*Oncorhynchus kisutch)* in the Buskin River, Alaska.

precipitation (mm) and average air temperature (C) recorded at the Kodiak Benny Benson State Airport, and yearly total run size. In-stream movements by adult fish totaled 451.5 km in 2015, 349.6 km in 2016, and 536 km in 2017. Finally, we found that precipitation (coefficient = 0.0012, p-value<0.0001) and air temperature (coefficient = -0.0047, p-value<0.0001) were influential variables in initiating freshwater movement, and air temperature a large component of lake utilization (p-value = 0.037). Ultimately, we found that Buskin River Coho Salmon fresh water entry timing has not shifted temporally, while the number of kilometers traveled in-river increased during high flow periods, and residence time increased with air temperature, suggesting the influence of trends in warming air and water may influence other aspects of migration beyond run timing.

Introduction

Understanding the patterns and processes that shape the distribution of animals in time and space is a fundamental goal of ecology. Animal movement can be influenced by interannual variation in climate (Peters and Lovejoy 1994; Mcloughlin and Ferguson 2000; Seebacher et al. 2014) and within season environmental factors (Roff 1980). Thus, understanding how animals respond to climate variation is critical towards understanding the potential for adaptive responses to rapid climate variation (Seebacher et al. 2014). Migration is a special form of movement that facilitates access to seasonally varying resources, for example skylarks' (*Alauda arvensis*) annual breeding migration cycle includes tradeoffs of energy in terms of food availability or lack thereof, the amount of time it takes to migrate the chosen distance, social structure, and diet based on location (Hegemann et al. 2012; Dingle 2014). Thus, migration strategies vary among and within species with regards to both timing and travel distances (Peters and Lovejoy 1994; Rivalan et al. 2007) as affected by the availability of resources, habitat fragmentation, and thermal variability (Bryant, 2009; Chevin et al. 2010; Crozier and Hutchings 2014). However, understanding the full role of climate on the timing of migration can be challenging for species that move across not only habitat boundaries, but entire ecosystems.

Anadromous fishes reproduce in freshwater, migrate to sea for a period of rearing, and then return to freshwater to spawn (Quinn 2018). The timing of anadromous fish migrations between freshwater and saltwater habitats as both juveniles and adults are thought to be critical transition periods between stages in their life history (Brannon 1987; Boatright et al. 2004; Quinn 2018). In particular, the timing of adult migration back to freshwater can be influenced by both genetic factors and the environment (Juanes et al. 2004; Crozier et al. 2011; Hinch et al. 2012; Kovach et al. 2015; Carey et al. 2017). Warming of freshwater environments can drive selective forces to shape both genetic and phenotypic adaptations (i.e., freshwater migration entrance timing) over time to all anadromous fish freshwater life history stages (Beamish et al. 1999; Halupka et al. 2000; Bryant 2009). Natural and anthropogenic factors including climate patterns, abundance, and fishing pressure can also influence migration timing on many levels (Keefer et al. 2008, Anderson and Beer 2009, Carey et al. 2017; Berdahl et al. 2018).

Climate can affect the migration of adult salmon across large, intermediate, and local scales, each of which is potentially influenced by different drivers. Ocean conditions and regimes can alter ocean migration timing, which plays a large role in long term salmon productivity (Lawson 2004; Anlauf-Dunn et al. 2014). Changes in large-scale ocean conditions, as reflected in the Pacific Decadal Oscillation (PDO), can affect the energy of salmon through food availability, in turn influencing freshwater entry timing (Cooke et al. 2004). The PDO is an oceanwide sea surface temperature condition index that has been shown to be correlated with changes in northeast Pacific marine ecosystems (Mantua et al. 1997). Several studies have suggested that ocean temperatures can dictate the energy levels of migrating fish and modify their route to their natal streams, potentially increasing the travel distance and delaying freshwater entry (Blackbourn 1987; Hodgson et al. 2006). Specifically, salmon use olfactory cues to return to their natal streams, but a wind-driven mixed water column layer can create a freshwater mixing barrier (Sea Surface Temperature (SST); Mundy and Evenson 2011; Smith and Reynolds 2003) adjacent to natal streams in the nearshore environment reducing the effectiveness of olfactory cues in salmon. Such olfactory cues which lead individual fish back to their natal rivers can become spatially isolated over time and leads to the plasticity of stock-specific adaptations to optimize variable conditions in individual rivers (Lohr and Bryant 1999; Kovach et al. 2015).

On a smaller and more localized scale, individual rivers have varying levels of sensitivity to climate variables which in turn influence biological patterns including fish movement (Rogers and Schindler 2011). These freshwater conditions are directly linked to spawning success and can directly affect all life history stages (Rand et al. 2006; Crozier et al. 2011; Kovach et al. 2015). Although the long-term pattern of freshwater entry timing is the product of an adaption of migration timing, modulated by freshwater conditions that allow access to spawning habitat and critical holding habitat (Quinn and Adams 1996; Cooke et al. 2004; Hodgson et al. 2006; Crozier et al. 2008, 2011). For example, local climatic variables such as flow and temperature can alter freshwater habitat significantly throughout a season, which can alter the distribution of salmon throughout the reaches of an individual river (Mull and Wilzbach 2007; Flitcroft et al. 2012; Anlauf-Dunn et al. 2014).

Understanding the relationships between climatic drivers and salmon migration on a local scale would enhance the management of salmon stocks. For some freshwater systems, climatic drivers may create high water events or thermally stressful conditions that may delay or expedite migratory behavior in salmon. For salmon systems, the lack of freshwater entrance timing predictability can create difficulties in managing for spawning escapements and subsistence and recreational opportunities (Hodgson et al. 2006; Mundy and Evenson 2011; Kovach et al. 2015). For example, fisheries managers can struggle with opening or restricting fisheries if they cannot accurately enumerate escapement during times of flooding. Thus, the ability to predict salmon freshwater entrance timing would have great applied utility to increasing a fishery manager's ability to conserve and utilize a stock to its greatest potential. Having a predicted date that 50% of the run should be in the river combined with the historical run timing curve would enhance a manager's ability to interrupt if the run was strong, weak or average.

In this paper we explore the environmental influences shaping adult Coho Salmon river entry and patterns of movement in the Buskin River, Kodiak Island, Alaska. We investigated connections between returning Coho Salmon freshwater entrance timing and in river movement with climate variables measured at regional-, staging area-, and freshwater-scales. Specifically, our objectives were to 1) quantify the extent of freshwater entrance timing change through time, 2) create a model that best explains timing of river entry based on climatic variables, and 3) quantify the influence of stream flow and temperature on in-stream movement, travel rates and use of holding habitats.

Methods

Study Area

Freshwater migration commences in mid-August, after the Buskin River lower weir is installed around August 1. The Buskin River watershed (57 °46'N, 152 °32'W) drains 67 km^2, and is approximately 10 km in length, which includes Buskin Lake located 5 km from the river mouth (Figure 2.1). The Buskin River watershed experiences a temperate marine climate with an average autumn (August-November) precipitation of 180 mm, an average autumn daily water temperature of 10°C (National Oceanic and Atmospheric Administration Weather https://www.ncdc.noaa.gov/cdo-web/datasets#GHCND), and daily average SST collected from a HOBO Water Temperature Pro v2 Data Logger in the nearshore estuary of Trident Basin, that had an autumn average of 10.5°C, approximately 6 km from the mouth of the Buskin River. In addition to Coho Salmon, the Buskin River also supports populations of Sockeye Salmon (*O. nerka*), Pink Salmon (*O. gorbuscha*), Chum Salmon (*O. keta*), Dolly Varden (*Salvelinus malma*), and Steelhead (*O. mykiss*).

Fish counts

An Alaska Department of Fish and Game (ADF&G) fish counting weir is located approximately 0.8 km upstream from the river mouth, operated from August 1 to September 30 (Figure 2.1); daily fish counts of Coho Salmon during this period were available from 1985 to 2018. Coho Salmon harvest levels were used to account for total sport fish removals from the Buskin River, from the ADF&G Sport Fish Statewide Harvest survey (SWHS), and Buskin near shore subsistence catch numbers from the Kodiak Commercial Fish Subsistence Database. The lower Buskin River weir is highly susceptible to high water events that make counting fish passage difficult and sometimes impossible at the highest flows.

Tagging and tracking

Upstream migrating adult Coho Salmon were captured in a live trap attached to the lower weir (Figure 2.1) between August 15 and September 30 during 2015, 2016, and 2017. The trap was opened on an ad hoc basis between 0700 and 2000 each day based on the number of fish observed behind the weir. To the extent possible, we sought to deploy 150 radio transmitters equally over the entire run. To proportionally tag throughout the run, we determined each day’s target number for tagging based on the percentage of the total long-term average escapement that passed through the weir on a given day. In all years, adaptive in-season modifications to the sampling goals were necessary to account for weir operations and weather conditions, as well as unprecedented low returns observed in 2016 (Polum and Stratton 2018).

Captured salmon were implanted with an Advanced Telemetry Systems (ATS) radio transmitter tag model F1845B, inserted through the esophagus and into the stomach, transmitting on one of five frequencies (149.634, 149.654, 149.655, 149.674, 149.694 MHz). Radio tags transmitted uniquely identifiable signals that were monitored with stationary and mobile receivers as described below. Tags were also customized with movement sensors that would send a signal if no movement had been detected for a 24-hour period, which was interpreted as mortality. All tagged Coho Salmon were also measured for length (mid-eye to tail fork; mm), sex was recorded and determined using external morphological features, a scale was taken for age determination, and a Floy t-bar tag was deployed to give an additional external marker.

We installed a tracking station at the lake weir to identify when tagged individuals entered Buskin Lake (Figure 2.1). The tracking station used an ATS model R4500 recording box and was affixed with antennas to monitor movements of radio tagged Coho Salmon. We installed additional tracking stations below the lower weir at a fishing platform to assess if Coho Salmon were falling back down river, over the weir. Another tracking station was added to the Battery Creek tributary to assess Coho Salmon movement into the tributary (Figure 1.1). We also installed a tracking tower on the nearby highway (Ace Cargo receiver; Figure 1.1) to assess whether tags were caught by anglers that subsequently exited the system by road without reporting.

To identify locations of fish in addition to the stationary receiver, we conducted weekly stream surveys using an ATS 4520C receiver throughout the watershed using a raft or on foot, depending on weather and river conditions. River surveys started after the first radio tag was deployed, starting at the lake weir and terminating at the lower weir. After the lower weir was removed around the end of September, surveys included the lower river due to the ability of Coho Salmon to drop down without the barrier of the weir in place. When the first radio tagged fish was detected past the lake weir station, we started weekly surveys of Buskin Lake using a raft. These surveys were conducted specifically at the outlets of the five major tributaries flowing into Buskin Lake after Coho Salmon were observed to have entered the tributaries. Locations of fish were determined from the strongest signal within 250 m of a receiver (ca. 250m, signal strength 250) and tag number, latitude, and longitude were recorded as closely to the fish location as possible. We aimed to be as exhaustive as possible in our surveys, although Devil's Creek, another major tributary of the Buskin River, was not surveyed as there is a complete barrier to fish passage where it flows under the Kodiak airport. Historically no Coho Salmon have been observed in the portion of Devil's Creek from the airport to its confluence with Buskin River (Polum and Stratton 2018). Fixed station and mobile tracking efforts continued until mortality signals were received for all individuals. Premature death was determined by mortality signals that were broadcast before spawning was observed to have initiated on approximately DOY 295 (October 22).

Environmental covariates

We used daily PDO averages from August through October to represent large scale ocean conditions that Coho Salmon migrated through from 1985 to 2018. Sea surface temperature (SST) monthly averages from August through October from ADF&G HOBO Water Temperature

Pro v2 Data Logger station located in Trident Basin (6 km from mouth of Buskin River; Figure 1) was used to represent staging area conditions that Coho Salmon migrating to the Buskin River would migrate through from 1985 to 2017. Historical precipitation (mm) and air temperature (C) data were used as proxies for stream flow and water temperature from 1985 to 2018 from the National Weather Service at the Kodiak Benny Benson State Airport station to represent local variables for migration. A stream gauge measuring water depth (mm) at the Buskin River lower weir site during the three years of the study (2015-2017) was utilized to check for correlation between precipitation and stream flow. A HOBO Water Temperature Pro v2 Data Logger located at the lower weir was used to check for a Pearson correlation between air temperature and water temperature. Precipitation and air temperature are good proxies for in-river conditions as precipitation was correlated to stream gauge readings ($r = 0.75$, p-value < 0.0001) and air temperature was correlated to water temperature ($r = 0.86$, p-value < 0.001).

Statistical analysis

Freshwater entrance timing across years

We explored four metrics of freshwater entrance timing to describe interannual variation and the influence of environmental forcing on patterns of river entry: the day of year in which 10% (DOY10), 50% (DOY50), 90% (DOY90) of the total annual run passed through the lower weir, and run duration (defined as the number of days between DOY10 and DOY90). Final weir count numbers were calculated using data obtained during the ADF&G Buskin River Coho Salmon project operational plan dates (August 1-September 30) to standardize weir counts. Both SWHS data and annual subsistence harvest data were used in addition to weir counts to calculate total run data (Table 1). Climate data were averaged to provide August, September, and October PDO, SST, precipitation, and air temperature. Thirteen weeks of weekly total precipitation levels (mm) and average temperatures (C) were calculated to compare to radio tag survey data in 2015, and twelve weeks of precipitation and temperature data for 2016 and 2017.

Freshwater entrance timing and climate relationship

A subset of 12 general linear models was created using the Program R (www.r-project.org) package AICcmodavg (Mazerolle 2019) to identify variables that best explained run date and duration variation given the data. Models were constructed with combinations of ocean (PDO), near shore (SST), and local variables (precipitation and air temperature) developed based on hypotheses. Climatic variables from the months of July and August were used. The model with the lowest AICc, lowest ΔAICc, and highest cumulative weight was considered the most parsimonious model and used for interpretation (Burnham and Anderson 2002). Regression diagnostics were performed to assess model assumptions and models were also assessed for autoregressive tendencies using ACF functions.

Influence of precipitation and temperature on in-stream movement, travel rates and holding

Survey data was reviewed to determine weekly locations of individual tagged Coho Salmon. Fish movement was assessed based on location of tags in comparison to the previous week's location. Linear regressions were used to evaluate the relationship between in-river fish movement, and weekly precipitation and air temperature. Final locations were determined as the reach within which the mortality signal was recorded. The week a fish reached its final spawning location was determined by the first week that the fish was observed in the same area that the mortality signal was recorded.

We modeled three metrics of in-river movement and holding as a function of the fixed effects of weekly precipitation and average air temperatures experienced during a focal week using mixed effect models created using Program R (www.r-project.org) package lme4 (Bates et al. 2015) and linear regression. First, we quantified whether fish were detected to have moved (coded dichotomously as 1=move, 0=stay) between river sections on weekly time steps, by fitting a logistic mixed effects models to account for individual tag movement. Second, movement was summed to produce a minimum estimate of total distance (km) moved for each tag, weekly totals for all tags in the river. Third, we defined lake residence as the number of days between the day fish entered and exited Buskin Lake based on information from the stationary lake tower. The second and third metrics both used linear regression to assess increases or decreases in arrival timing on spawning grounds or lake residence time relative to air temperature and precipitation.

Results

Freshwater entrance timing across years

Overall, Coho Salmon freshwater entrance timing in the Buskin River varied markedly across the 33-year data set, but no trends through time of earlier or later return were detected for each of the data sets (Table 2). The DOY10 ranged from 227 (August 15) to 260 (September 17) but the average was relatively stable, shown through a liner regression of DOY10 vs year (β=-0.102, r^2=0.02, p-value = 0.42), while DOY90 ranged from 256 (September 16) to 272 (September 29), the average also staying stable shown through a linear regression DOY90 vs year (β=0.034, r^2=0.007, p-value = 0.63). The DOY50 vs year linear regression showed that DOY50 did not shift in time (r^2=0.01, p-value = 0.53), yet it did range from 243 (August 31) to 272 (September 29). Run durations ranged from 12 to 43 days (β=0.08, r^2=0.036, p-value = 0.28). All DOY linear regressions were autocorrelated, however, all regression models were not statistically significant.

Freshwater entrance timing and climate relationship

The DOY10, DOY50, and DOY90 run date and run duration were explored as response variables and returned qualitatively similar results. Thus, we report results using only the 50% run date. The best fit model was SST alone (AICc= 217.56, Delta_AICc = 0.00, AICcWT = 0.66; Figure 4), however, this explained very little of the variation (r^2 =0.0085). We detected the largest role of regional and local scale SST in explaining freshwater entrance timing with SST present in all weighted models ($p < 0.05$), followed by a model with SST and PDO (AICc = 219.98, Delta_AICc = 2.42, AICcWT = 0.2) showing the importance of ocean variables to Coho Salmon freshwater entrance timing. The full model including PDO, SST, precipitation, temperature, and total run represented 24% of the variation in run date (r^2 = 0.24, AICc = 221.4, Delta_AICc = 3.84, AICcWT = 0.09).

Identify if the influence of precipitation and temperature on in-stream movement, travel rates, and holding

Out of 92 radio tags that were deployed in 2015, 75 radio tagged Coho Salmon moved a total of 451.5 km. In 2016, 96 radio tags were deployed of which 75 produced movement data resulting in 349.56 km, while in 2017, 160 deployed tags led to a total of 120 radio tagged Coho Salmon that moved a total of 536 km.

Movement of adult Coho Salmon increased during weeks with greater precipitation levels compared to weeks of lower precipitation (coefficient = 0.0012, odds ratio = 1.004, p-value <0.001; Figure 5). Holding increased during weeks with warmer temperatures (coefficient = -0.0.047, odds ratio = 0.094, p-value <0.001). A linear regression showed that distance moved in weeks with greater rainfall was statistically significant (r^2 = 0.01, p-value 0.0067). In contrast, air temperature was not statistically significant with increased distance moved (r^2 = 1.31^{e-06}, p-value = 0.9762). We note, however, that the amount of variation of movement explained by precipitation was very low ($r^2 = 0.01$). We found that precipitation and air temperature were not highly correlated for August, September or October (r = -0.288, -0.314, 0.435) so all regression models were completed with both precipitation and temperature.

Colder air temperatures were statistically significant with earlier arrival week to spawning locations ($r^2 = 0.001$, p-value = 0.05691), although, precipitation was not a significant factor in the week of arrival on spawning locations ($r^2 = 3.033e^{-10}$, p-value =0.99). The number of days of lake residence time increased with temperature ($r^2 = 0.0025$, p-value = 0.037). The day Coho Salmon entered the lake was earlier with greater precipitation amounts (p value = 0.016). However, the day Coho Salmon exited the lake was not associated with increased precipitation levels (p-value = 0.259) or temperature (p-value = 0.525).

Discussion

Analyses of 33 years of migration timing data and three years of telemetry tracking of adult Coho Salmon in this project revealed the following salient points. First, Buskin River Coho Salmon freshwater entrance timing, while highly variable, showed no temporal trend towards earlier or later dates. This contrasts with several recent reports from other species and regions of shifts in run timing potentially associated with climate change (Quinn and Adams 1997; Cooke et al. 2004; Hodgson et al. 2006; Crozier et al. 2008, 2011; Kovach et al. 2012, 2013, 2015). Second, nearshore SST was found to be a primary driver of freshwater entrance timing as later entrance timing was associated with warmer SST in Trident Basin. Third, precipitation as a proxy for stream flow and air temperature as a proxy for water temperature were found to have a significant relationship with the increased amounts of movement and holding of Coho Salmon in the Buskin River. Air temperature, as a proxy for water temperature, was also found to be associated with use of the lake. This study reinforced the assumption that Coho Salmon travel in-river during times of high flow in the Buskin River and corroborated mounting evidence of the importance of Buskin Lake as holding habitat (Stratton et al. *in-prep*) given fish tend to migrate to the lake earlier during warm periods. These results have implications for management of the system, particularly as related to the challenge of enumerating escapement as salmon move when stream flows are high, making counting and maintaining weirs difficult.

Other studies of salmon migration timing have found that freshwater entry timing is in fact adapting in response to a changing climate (Stafford et al. 2000; Wing et al. 2006; Crozer et al. 2011; Kovach et al. 2012; Carey et al. 2017). For example, a multitude of Sockeye Salmon stocks are migrating earlier in the Columbia River and Fraser River (Quinn and Adams 1997; Cooke et al. 2004; Crozier et al. 2011), along with Pink Salmon and Coho Salmon in Auke Creek (Taylor 2008; Kovach et al. 2013), while other fish populations are migrating later in the season (Carlson et al. 2011; Crozier et al. 2011; Kovach et al. 2012). With changes to salmon migration timing a topic of current research, fisheries managers should keep in mind that not all stocks are reacting the same in response to environmental variables. Understanding the drivers behind entrance timing and freshwater movement in individual rivers can lead to more informed fisheries management in the future by an increased knowledge of how the fish generally act in certain water flows and temperatures (Cooke et al. 2004; Taylor 2008; Kovach et al. 2013).

The duration of the Buskin Coho Salmon run appeared inversely proportional to abundance. In years of higher abundance, the run was more contracted offering fewer days that fish were available to be caught in the near shore subsistence fishery and the freshwater sport fishery. Larger run sizes not only increase the quality of subsistence and sport fisheries of a river but have been found to collectively increase the homing success through the ocean and encourage earlier freshwater migration dates, while increasing the group's ability to track environmental gradients, which increases the probability of successful navigation (Berdahl et al. 2016). Carey et al. (2017) found that over 11 years, run size had a positive relationship to the duration of the Pilgrim River Sockeye Salmon run. Yet, no relationships were found between abundance and run duration for Sockeye Salmon in the Columbia River over 60 years (Crozer et al. 2011). Kovach et al. (2015) showed that for some populations of Coho Salmon, run duration has decreased by approximately two weeks. Other systems are showing adaptations to climate change, but the Buskin River is staying relativity consistent through time, possibly due to different climate filters on a smaller system.

Best estimates were used in place of weir counts during times that the weir was not operational due to floods. Post flood river surveys can be used to survey the amount of Coho Salmon between the two weirs. It was thought that fish moved most during flood events due to the rising water levels giving access to whole river sections and tributaries. We have shown Coho Salmon in the Buskin River, Kodiak, Alaska movement increases with high precipitation levels.

We created a set of models to evaluate the influence of a large-scale ocean variable (PDO), an intermediate-scale near shore variable (SST), and freshwater variables on freshwater entrance timing. Although we were able to infer the role of multiple drivers, the full model that included SST, PDO, precipitation, air temperature, total run, and year was only able to account for 24% of the freshwater entrance timing variations and 9% of the model weights, indicating substantial variation was not captured by our model. All highly weighed models included SST, suggesting that near shore environmental conditions are important to the freshwater migration timing of Buskin River Coho Salmon. Nearshore Sea Surface Temperature was also an important factor in freshwater migration timing of Pilgrim River Sockeye Salmon (Carey et al. 2017) and Chinook Salmon in the Columbia River (Keefer et al. 2008). It has been noted that nearshore SST in the spring can act as a trigger that initiates freshwater entrance and accounts for migration schedule and fish maturation (Meyers et al. 2007; Carey et al. 2017). Similarly, Kovach et al. (2015) found that their models could not account for the changes in migration timing of Coho Salmon, Chum Salmon, and Pink Salmon populations using PDO, SST, precipitation and temperature as variables. As SST increased in the near shore waters surrounding the Buskin River, Coho Salmon freshwater entrance dates were later in the season than in years with cooler SSTs. Meyers (et al. 2007) proposed that spring SST can activate and affect migration rates and timing, and Mundy and Evenson (2011) found that near shore environment interannual variation was correlated with triggering freshwater migration.

The models produced did not predict a DOY50 run date that could be used to manage the run. A fishery manager's knowledge of early, late, weak, or strong run timing would provide a greater understanding of the run's behavior and a greater ability to closely manage the run to meet escapement objectives. The best fit 50% run date models included PDO, showing the influence of ocean variables. When investigating PDO and SST, these variables had low correlation showing that could have influence separately on migration timing. Cooke (et al. 2004) found that ocean variables have effects on fish arriving at nearshore environments outside natal river and influential in the decision to enter freshwater. PDO also was significant to freshwater migration timing of Columbia River Chinook salmon and Sockeye Salmon (Crozier et al. 2011; Keefer et al. 2008).

In-river salmon migration movements can be broken down into multiple phases: a period of rapid upstream movement (Anderson and Quinn 2007), a searching phase that includes both upriver and downriver movements (Okland et al. 2001), and final spawning movements (Anderson and Quinn 2007). Environmental factors like stream flow and temperature affecting salmon migration has been studied for decades (Davidson et al. 1943; Shapovalov and Taft 1954; Banks 1969; Anderson and Quinn 2007). In the Buskin River, years with less precipitation generally had higher sport and subsistence harvest rates (Table 2.1), consistent with the idea that extended holding in the river or nearshore may come at a survival risk. In 2015, the Buskin River experienced very little precipitation early in the season (Figure 5) and most of the river was inaccessible to the Coho Salmon, forcing fish to hold in the near shore environment and tidal section of the river until later in the season (Polum and Stratton 2018). In 2016, consistent precipitation events through the season created open access to all sections of the river throughout the entire season. Precipitation conditions in 2017 were intermediate between 2015 and 2016 conditions and access to the river was not as restricted. Shifting abiotic environmental conditions have been shown to affect migration timing in Sockeye, Chum, and Coho Salmon (Quinn et al 2002; Hinch et al. 2012; Kovach et al. 2012, 2013). Although our model could not predict the DOY50, it is apparent that environmental cues affect the migration of Coho Salmon in the Buskin River.

In-river environmental conditions have been shown to be influential to freshwater migration timing for Sockeye Salmon in multiple rivers (Taylor 1991; Quinn et al. 1997; Cooke et al. 2004; Hodgeson et al. 2006). We found that fish movement increased with precipitation or air temperature. This relationship is logical due to low water creating barriers to certain sections of the Buskin watershed. As a results, greater precipitation during a season leads to more of the river being accessible. Many rivers are known for different flow and temperature patterns that affect entrance and spawn timing based on the location of the river, generally mountain regions have drier patterns while coastal rivers tend to be wetter (Busby et al. 1996; Robards and Quinn 2002). Lake entrance date was also found to be related to with precipitation levels; higher amounts of rain drew more Coho Salmon up the river and into the lake. In all cases, higher precipitation invoked Coho Salmon to move, while increasing temperatures encouraged utilization of the lake and holding as the lake could be a safer area from fishing pressure and predators.

Conclusions and Management Applications

Freshwater migration timing is a significant facet of reproduction that is the culmination of all the environmental drivers fish encountered throughout the entire migration (Crozier et al. 2011; Kovach et al. 2015; Carey et al. 2017). Identifying the relative importance of large-scale ocean and intermediate-scale near shore freshwater migration timing drivers is the first step to understanding Buskin River Coho Salmon migration behavior. Once in the Buskin River, knowing that fish move during high water events can serve as the starting point of determining how to best estimate Coho Salmon weir counts during times of outage.

The functionality of a model that accurately predicted the 50% run date based on climate variables would have been invaluable to a salmon manager for inseason management to better understand run strength and timing for comparison to the current year's weir counts and escapement objectives. The model we produced was not able to capture a substantial amount of variation of the 50% run date throughout the years and is thus unlikely to be of major management utility. Although a model that could be used in season with predictive power was not produced, we determined that ocean variables emerged as important in freshwater migration timing. This novel finding in this system forms the basis for future extended efforts to model run timing.

The marked variability in timing of Buskin River coho salmon freshwater entrance timing makes it difficult to infer any compelling patterns out of size or run strength in season. Said another way, the variability in run timing can make early, small runs look large, and large, late runs look small. Fish entering the river earlier and the potential of the run being protracted provides more angler days for subsistence and sport fishermen, along with the potential of overfishing. The earlier entering fish will seek safe holding habitats until suitable spawning conditions become available. Safe holding habitats in the Buskin River watershed also align with areas of higher fishing pressure (Stratton and Evans *in-prep)*. With this overlapping habitat, fish that enter earlier have the highest probability of being caught. Possible management options to address overfishing when conservation is necessary includes restricting fishing above the weir to gain a better understanding of fish in the river and adding post flood surveys accounting for the high number of estimated counts.

Due to the flashy flow regime of the Buskin River keeping the weir in for the entire season has proved unrealistic. During recent years, innovative new designs to the weir to increase the weir's ability to stay operational with higher stream flows have been implemented. These improvements have been successful with keeping the weir in through higher stream flows, but still has limits. This study showed that during periods of high flow, Coho Salmon increase their movement. This leads to fish moving up-river when the weir is not operational and fisheries managers requiring a reliable method to estimate fish passage.

Throughout the three years of this study, precipitation levels had an impact on distance moved, holding times, and lake residence. Fish moved more and utilized the lake with higher precipitation levels. The Buskin River sees high levels of precipitation throughout the year and is highest in the fall months when adult Coho Salmon are present. Knowing how Coho Salmon generally react to crossing different scaled habitats can increase our ability to predict freshwater entry patterns in the future, while understanding in river movement through stream flow and temperature will increase the ability to manage for the protection Coho Salmon in stable holding habitats. Future work in modelling could improve understanding run timing and movement including more variables to account for greater levels of variation.

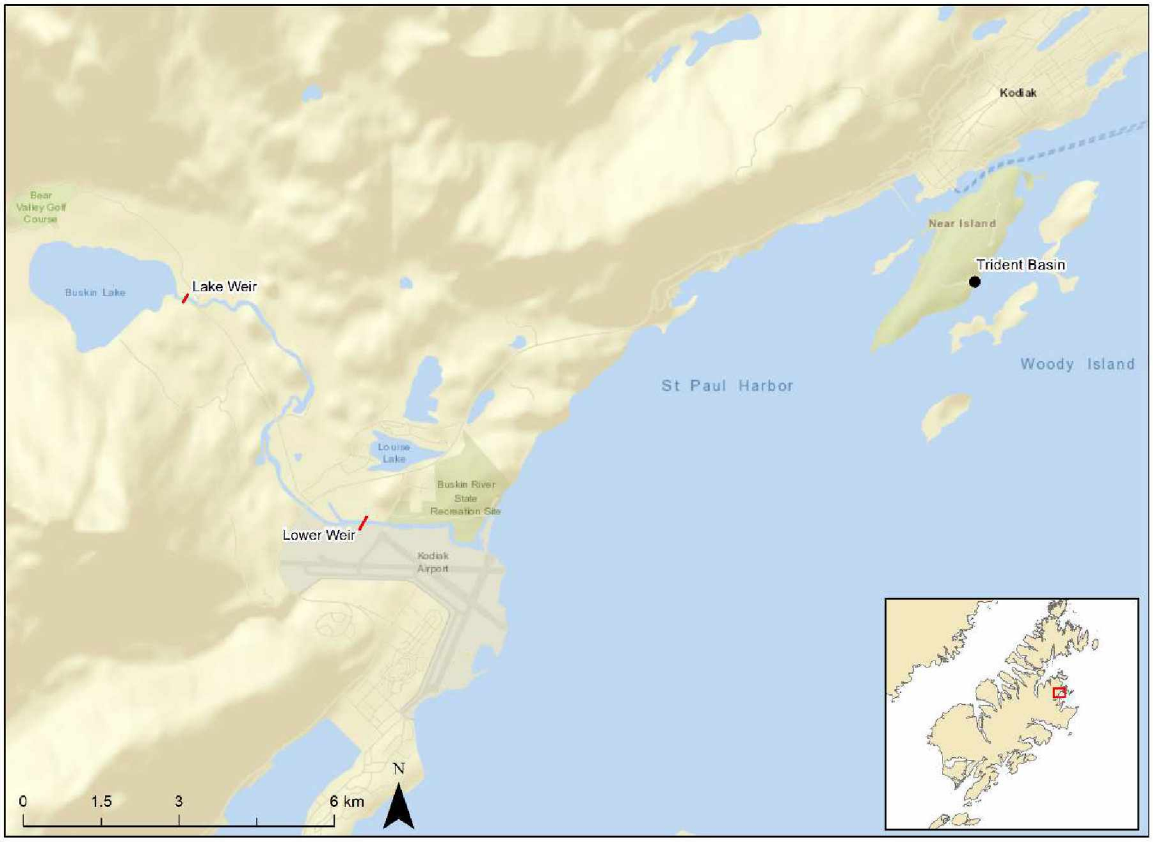

FIGURE 2.1 Map of the Buskin River watershed, Kodiak Island, Alaska (57 °46'N, 152 °32'W), showing the watershed, weir locations, and Trident Basin.

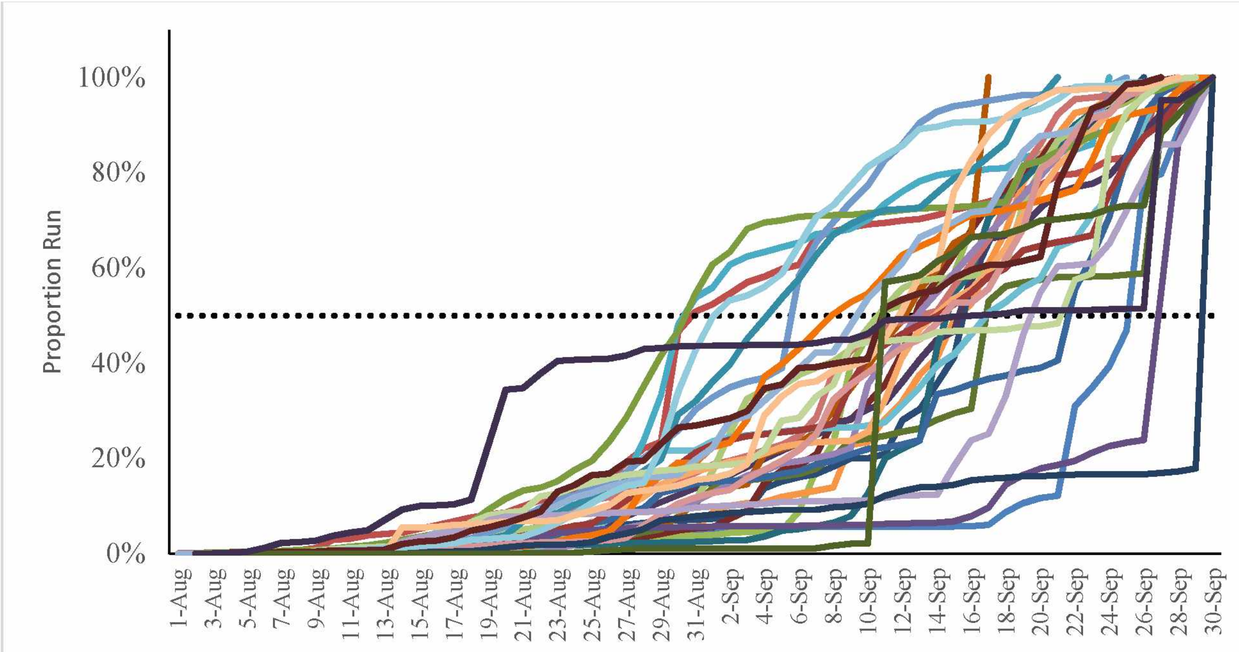

FIGURE 2.2 Buskin River Coho Salmon cumulative run timing plot for 1985 to 2018 with 50% marked with dotted horizontal line.

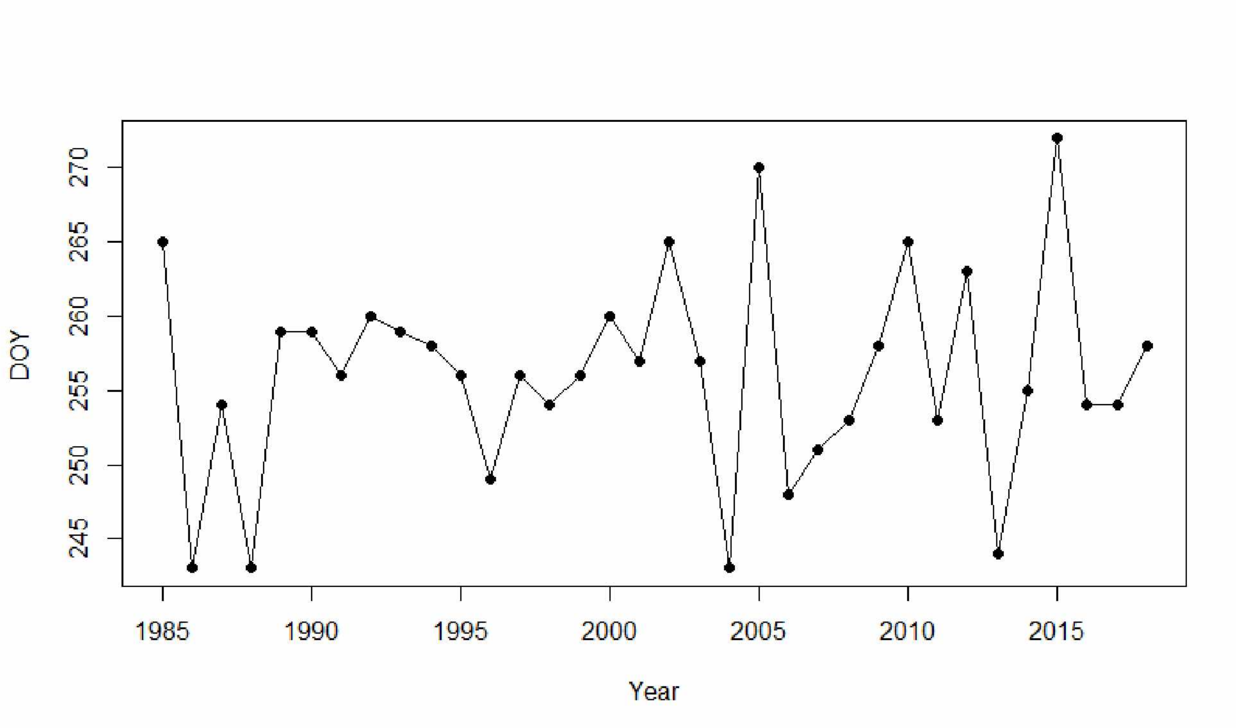

FIGURE 2.3 Buskin River Coho Salmon 50% run dates from 1985 to 2018. For reference DOY 245 corresponds to September 2 and DOY 270 corresponds to September 27.

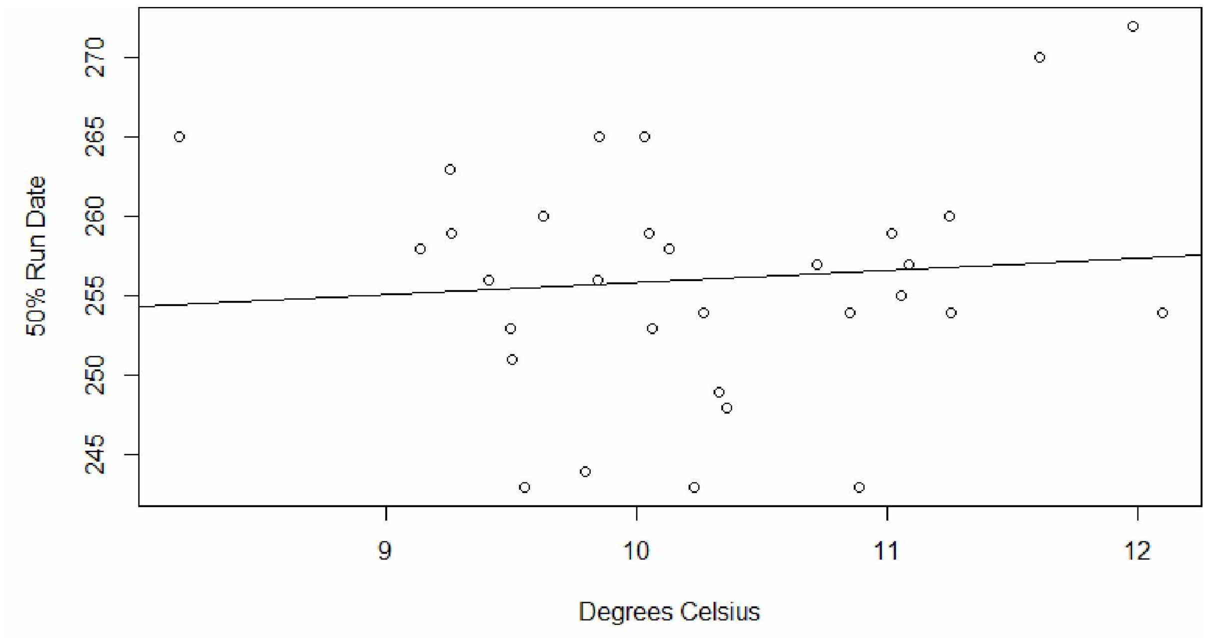

FIGURE 2.4 DOY50 Buskin River Coho Salmon counted with SST (°C) from Trident Basin.

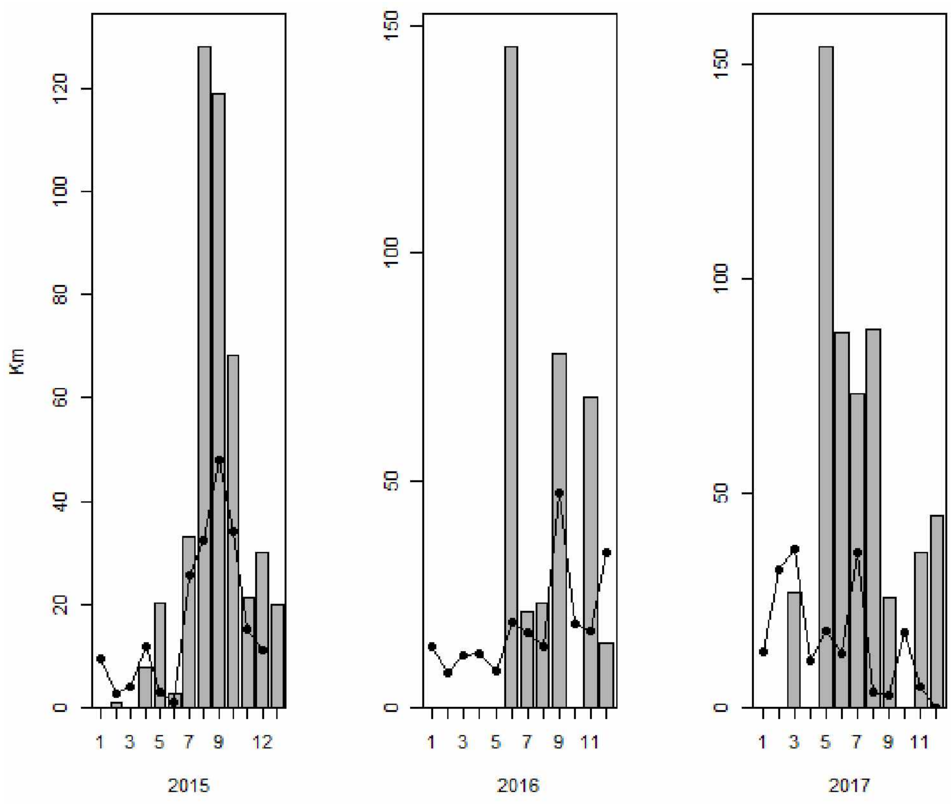

FIGURE 2.5 Kilometers moved by tagged Coho Salmon (left y axis) along with weekly precipitation totals (mm; right y-axis) as a function of date (week).

TABLE 2.1 Weir count data of Coho Salmon from the lower Buskin Weir, Buskin River sport fish harvest from SWHS, subsistence harvest from Kodiak Commercial fish database in 2015, 2016, and 2017.

Year	Weir count	SF harvest	Subsistence harvest	Total run
2015	904	4,889	884	6,677
2016	2,488	1,895	496	4,879
2017	5,559	2,337	300	8,196

TABLE 2.2 Buskin River Coho Salmon minimum, mean, and maximum run dates between 1985 and 2018.

Year	Minimum	Mean	Maximum
10% run	231 (Aug 19)	242 (Aug 30)	273 (Sept 30)
50% run	242 (Aug 30)	257 (Sept 14)	279 (Oct 5)
90% run	256 (Sept 13)	268 (Sept 25)	281 (Oct 8)

TABLE 2.3 Model selection based on Second-order Akaike Information Criterion (AICc) of Buskin River Coho Salmon run timing variation using August variables (Sea Surface Temp (SST), Pacific Decadal Oscillation (PDO), precipitation, and air temperature), total run, year. Number of parameters in model (K).

Model	K	AICc	Delta_AICc	AICcWt	r^2
SST	3	217.5604	0	0.6648	0.0086
SST+PDO	4	219.9783	2.418	0.1985	0.0169
SST+PDO+PRECIP+TEMP+TOTAL RUN	7	221.3959	3.8356	0.0977	0.2377
SST+PDO+PRECIP+TEMP+TOTAL RUN+YEAR	8	223.37	5.8096	0.0364	0.2784
PRECIP	3	230.9099	13.3496	0.0008	0.1157
PRECIP+TEMP	4	231.6829	14.1225	0.0006	0.1614
PRECIP+TEMP+TR	5	232.6427	15.0823	0.0004	0.2048
NULL MODEL	2	232.6773	15.1169	0.0003	0
TOTAL RUN	3	234.6056	17.0452	0.0001	0.0142
YEAR	3	234.6577	17.0973	0.0001	0.0126
TEMP	3	234.6996	17.1393	0.0001	0.01142
PDO	3	234.7555	17.1951	0.0001	0.0098

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Conclusions

The overarching goal of this thesis was to illuminate the reproductive ecology of Coho Salmon (*O. kisutch)* in a small coastal watershed that supports vital and vibrant sport and subsistence fisheries. The Buskin River watershed, Kodiak Island, AK was a good candidate for a study system due to its proximity to the city of Kodiak, AK and relative ease of access to most of the river. I analyzed the timing of migration into freshwater of Buskin River Coho Salmon, and the in river movement patterns, increasing the understanding of this important subsistence and recreational stock's patterns of migration and increased the knowledge of best management practices for abundance and conservation in the future. The fundamental findings of this thesis include the following:

- In a small, coastal watershed the early entering Coho Salmon do not always travel the farthest as previously thought.
- Lakes can provide critical holding habitats for both tributary and main stem spawning Coho Salmon.
- The Buskin River Coho Salmon population has not shifted run timing earlier or later in response to changing climatic factors. There may be year to year variation, but overall, freshwater run timing did not exhibit a trend in date.
- Ocean and near shore drivers PDO and SST can have strong influences on initiating river entrance timing.
- Precipitation and temperature were river movement drivers that can be used to understand when large pulses of fish will initiate movement.

Buskin River watershed management applications

Due to the Buskin River watershed's proximity to the city of Kodiak, AK, the Coho Salmon stock wields great subsistence and recreational fishing importance. The lower weir used to count Coho Salmon into the river allows managers to make in-season management decisions. Due to the flash flood nature of this watershed, many of the daily weir counts are compromised and best practice estimates replace physical weir counts on days the weir is non-operational. The introduction of estimates to the counts undoubtedly increases variability in the dataset and makes it more challenging to detect signals of environmental forcing. The Buskin River Coho Salmon escapement goals were established as a Sustainable Escapement Goal (SEG) at 6,000 to 9,000 fish in 1999 (Nelson and Llyod 2001). Sustainable Escapement Goals are sustainable levels of escapement indicated by an index of escapement (Schaberg et al. 20016). Generally, SEGs are determined by a Percentile Approach (Clark et al. 2014) that establishes a range based on observed escapement relative to data contrast, harvest rate, and measurement error associated with the data (Schaberg et al. 2016). The goal was reevaluated in 2005 and changed to a Biological Escapement Goal (BEG) of 3,200 to 7,200 fish (Nelson et al. 2005). BEGs are established using spawner-recruit models based on run reconstructions which provide spawner estimates necessary to achieve maximum sustained yield (Hilborn and Walters 1992). This new method was an attempt to account for 20% of sport harvest occurring above the lower Coho Salmon weir (Schaberg et al. 2016). Finally, an updated brood table and spawner-recruit analysis were utilized to change the BEG to its current goal of 4,700 to 9,600 fish (Sagalkin et al. 2013).

Management options to achieve escapement goals include an increase, decrease, or closure of the daily Coho Salmon sport fish bag limit, and a liberalization or closure of waters near the mouth of the Buskin to subsistence fishing. As fish migrate into freshwater, managers look to the weir counts to evaluate the strength of the run and make management decisions based on these numbers. Murray (1987) determined that 20% of the sport fish harvest takes place above the lower weir. This means that when evaluating the weir counts, the true escapement number would be estimated at approximately 20% lower than the total weir counts. Conceivably, in-river estimates would be more appropriate than weir counts alone to account for missing weir counts and the reduction in escapement from the sportfish harvest. The popular in-river Coho Salmon sport fishing locations overlap with the critical holding habitat identified in this study; Buskin Lake, Beaver Pond, Island Hole, and Pumphouse all receive substantial Coho Salmon fishing pressure and have the highest probability of having holding fish seeking protection from predators. Years that have lower weir counts could prove problematic when higher fishing pressure occurs within the same habitats that fish seek refuge.

We found that freshwater entrance timing was similar for both tributary and main stem spawning fish. The management application from this finding is that heavier fishing pressure at any point throughout the run should not threaten either of the two components that make up the Buskin River Coho Salmon stock. If either spawning location component had a different run timing, a manager would have to be sensitive to the timing of fishing pressure to not overfish a single component. Similarly, fish length did not differ between the spawning locations. Sport fishing and net size selectivity would be a concern if the concentration of large fish spawned in a location while smaller sized fish spawned in the other. Within a single year if the amount of tributary spawners or main stem spawners increased, the overall total run count could remain unchanged if the other portion decreased, in a population structure portfolio effect. Indeed, in the three years of tracking where the fraction of main stem vs. tributary spawners is estimated, we see the range of 39% to 53% tributary spawners suggesting a buffering influence on total productivity.

Changing climate implications

It has been documented that the warming global climate is presenting new challenges for salmonid fishes in marine and freshwater habitats (Casselman 2002; Sharma et al. 2007; Isaak et al. 2010; Hartmann et al. 2013). Pacific salmon can adjust to environmental changes through adaptive plasticity to increase their likelihood of survival (Bryant 2009; Chen et al. 2016; Poesch et al. 2016). Reproductive success is dependent on adaptive strategies that increase the probability of migrating through favorable environmental conditions (Hodgson and Quinn 2002; Portner and Peck 2010; Chiaramonte et al. 2016). Bridging the alterations made to migration timing through multiple climate scales can increase our ability to manage individual stocks (Keefer et al. 2008, Anderson and Beer 2009, Berdahl et al. 2018).

Migration timing into freshwater is thought to be a critical transition period for adult salmon (Brannon 1987;Boatright et al. 2004; Quinn 2018). We found that the Buskin River freshwater entry timing has varied over between 1985 to 2018 but has not shifted towards a new entrance timing. Our results show that nearshore SST in August is the most significant driver of freshwater entry timing of this stock. The full model we created accounted for 24% of entrance timing variation and revealed that inferences could be made from ocean variables (SST and PDO of August). Therefore, managers of this fishery can look towards these variables as an indicator of potential early or late run timing to assist in judging run strength. The utility of a model that could accurately predict 50% run date would be invaluable to fisheries managers, but a model with this utility was not able to be created. It was confirmed that fish have higher rates of movement with greater amounts of stream flow, giving insight to when fish potentially enter and migrate up river during times the weir is not functioning due to high water.

Once in freshwater, stream flow was a driver of in-river movement. In weeks that saw greater flow rates, the number of radio tagged Coho Salmon and distance moved increased. Managers can use this information as a starting point to develop an accurate method to estimate fish passage during the periods the weir is non-functional. Air temperature was also a significant driver for Coho Salmon to initiate holding in or exit holding areas. Since critical holding areas overlap with popular fishing locations, it is important to understand that with warmer temperatures fish are at greater risk of harvest.

Comments for future work

Expanding the knowledge of how small coastal Coho Salmon rivers react to changing climate relative to longer rivers would be a useful tool for Alaskan stock fisheries managers. An immediate change to managing the Buskin Coho Salmon stock resulting from this thesis was the elimination of the lake weir after August. Coho Salmon migrate to the lake, hold, and return to the main stem of the river, removing the assumption that all lake fish utilize the upper tributaries. Studying watersheds similar to the Buskin River can continue to increase our knowledge of how smaller systems work, which would be beneficial to the many small coastal Coho Salmon runs on Kodiak. Further investigation could be worthwhile to look at why fish that spawn in the mainstem migrate past their spawning area, hold in the lake, and return to the mainstem of the river. Within the Buskin River, an accurate way to estimate Coho Salmon passage during high flow periods when the weir is out is still necessary. Escapement estimates made from incomplete weir counts are generally based on run strength and freshwater entrance timing. It is also unclear whether genetic differences exist between tributary and main stem spawners, which could point towards a higher level of population structure. Despite the current lack of data on genetic differences it is prudent to continue management strategies and habitat protection that preserve current levels of diversity in this small watershed.

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